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Utah Shrub Ecology Workshop
The Genus *Cercocarpus*

Logan, Utah
July, 1988

College of Natural Resources
Utah State University, Logan

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July 13-14, 1988

Editor: Kendall L. Johnson
Extension Range Specialist

College of Natural Resources
Utah State University
Logan, Utah 84322
1990

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1988

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The Utah Shrub Ecology Workshop

The State of Utah lies athwart two physiographic provinces, the Colorado Plateau and the Great Basin. In both provinces, shrublands are the vegetative type forming an overwhelming majority of the total land area. It is fair to say that in Utah rangeland is shrubland, hence shrubs occupy a central position in the ecology of the state for livestock grazing, wildlife habitat, water production and many other uses. In view of their importance, the Utah Shrub Ecology Workshop was established in 1981 to enable searching examination of the ecology, uses and management of shrublands. It draws together professional range and wildlife specialists for evaluation and discussion of current research and management programs.

The Workshop is sponsored jointly by Utah State University, USDA Forest Service, USDA Intermountain Research Station, USDA Soil Conservation Service, USDI Bureau of Land Management, Utah Division of State Lands & Forestry, and Utah Division of Wildlife Resources. Direction of the workshop is by a steering committee, composed of a delegate from each support agency.

Normally, the workshop centers on a specific shrub type each year, selected by the steering committee. The workshop has a total length of 1 1/2 to 2 days. A formal session, held during the first day, allows presentation of papers devoted to research and management programs. A field trip on the second day provides examination of shrub ecology and management problems. Open discussion is encouraged throughout the program. To preserve the workshop atmosphere, attendance is normally limited to about 45 persons. Participants are designated by their agencies upon invitation from the steering committee. Registration is set to defray meeting expenses, including publication of papers in formal proceedings. The structure follows a pattern set by the Wyoming Shrub Ecology Workshop.

The 1988 Workshop was devoted to examination of the taxonomy, ecology and management of the three species of mountain mahogany (*Cercocarpus*) occurring in Utah. Participants learned of the likely evolutionary development of mountain mahogany in Utah, general ecology and some ecophysiological characteristics of the genus, and response of curlleaf mountain mahogany to management programs. The field chairmen were Roger E. Banner of Utah State University and A. H. Winward of the U. S. Forest Service. The steering committee acknowledges the direct support of USU in staging the workshop.

This volume records the activities of the fifth Utah Shrub Ecology Workshop in order to extend its benefits to a wider audience than the technicians attending the workshop itself. Its preparation, like all of the preceding volumes, was largely accomplished through the dedicated service of Roma Henderson, Administrative Secretary, Department of Range Science, Utah State University. The steering committee acknowledges its debt to Mrs. Henderson for her many efforts in behalf of the Workshop, particularly Kendall Johnson, whose responsibilities as Coordinator and Editor could not have been accomplished without services she so willingly provided.

Kendall L. Johnson
Editor

Session 1: Management of Utah Shrublands

GENERAL ECOLOGY, WILDLIFE USE, AND MANAGEMENT OF THE MOUNTAIN MAHOGANIES IN THE INTERMOUNTAIN WEST

James N. Davis

ABSTRACT: As a group, Cercocarpus H.B.K. (mountain mahoganies) are shrubs or small trees that commonly occupy the dryer sites of the interior mountainous regions of western North America. Relatively little autecological information is available about the genus, but all species provide important browse or cover for many big game populations. Two of the more widely distributed and utilized species are curlleaf mountain mahogany (C. ledifolius) and true mountain mahogany (C. montanus). A third species, little leaf mountain mahogany (C. intricatus) has a much more restricted habitat.

Generally, these species can be found at elevations ranging from about 800 to over 3,200 m with lower altitude preferences near their northern range limit. They are normally found on warm, dry, rocky ridges or plateaus on all exposures, but primarily western or southern aspects. True mountain mahogany communities can usually be found at lower elevations than curlleaf mahogany, occurring on similar slopes but usually with deeper soils. Little leaf mahogany is ecologically a bit of a mystery because of its more restricted habitat. It appears to thrive on very shallow soils or in cracks and crevices of rock outcrops on rimrock, cliffs, and rocky dry slopes within desert shrub, pinyon-juniper, and mountain brush communities. Both curlleaf and true mountain mahoganies are highly palatable winter browse for elk and deer. Curlleaf is one of the few browse species that meet or exceed the protein requirements for wintering big game animals.

True mountain mahogany offers several management options due to its resprouting nature and lower elevational range, while management of the non-sprouting, evergreen and higher elevation

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curlleaf is much more restricted. The limited occurrence of little leaf mountain mahogany on harsh sites rules out most management options.

ACKNOWLEDGMENTS: Federal funds for wildlife restoration were provided through Pittman-Robertson Project W-82-R, studies 1 and 2. Work was done in cooperation between the Utah State Division of Wildlife Resources and the Intermountain Research Station, Forest Service, U.S. Department of Agriculture.

INTRODUCTION

Species of the genus Cercocarpus, commonly called mountain mahogany, are shrubs or small trees occupying dryer sites of the interior mountainous regions of western North America. All species provide important browse or cover for many forms of wildlife, especially big game. Three major species occur in the Intermountain and Great Basin regions (Holmgren 1987, Welsh et al. 1987). Two widely distributed and utilized species are curlleaf mountain mahogany (C. ledifolius) and true mountain mahogany (C. montanus). A third species, little leaf mountain mahogany (C. intricatus), has a more restricted habitat. Where any two occur together, hybrids often result. Great amounts of variation in growth form and leaf size occur within any one of the species on most sites. Relatively little autecological information is available in the literature on curlleaf mountain mahogany, even less on true mountain mahogany, and almost none on little leaf mountain mahogany.

CURLLEAF MOUNTAIN MAHOGANY

Curlleaf mountain mahogany is the largest and most widely distributed of the three species. Figure 1 shows its occurrence in all of the western states except New Mexico (Martin 1950). Holmgren (1987) recognizes two varieties: var ledifolius with narrow leaves and var intermontanus with broad leaves. Although this discussion does not distinguish between the two varieties of curlleaf mountain mahogany, the narrow-leafed var ledifolius is widely distributed throughout the more northern and eastern portions of the species range, while the wide-leafed var intermontanus is commonly more western and southern in its distributional limits. The varieties overlap through the central portions of curlleaf range.

Curlleaf mountain mahogany is an evergreen, montane xerophyte normally found as a small tree but sometimes occurring as a large shrub. Average heights range from almost 2 m in Montana to 9 m or more in Utah. It is most frequently associated with the sagebrush, pinyon-juniper, mountain brush, ponderosa pine, and spruce-fir zones (Martin 1950). It can also take the place of ponderosa pine (Pinus ponderosa) and aspen (Populus tremuloides) at intermediate elevations in central Nevada (Tidestrom 1925). Curlleaf mountain mahogany actually occupies a narrow but unique position between the lower fringes of the conifer zone and the upper edges of the desert steppe. The best developed stands are routinely found on warm, dry, rocky ridges or slopes on all

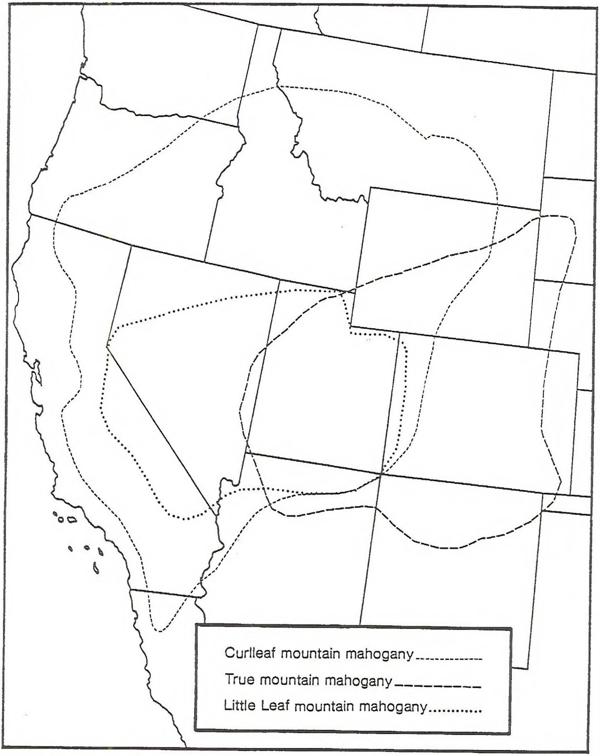

Figure 1. Distribution of curlleaf mountain mahogany, true mountain mahogany, and little leaf mountain mahogany.

exposures (primarily western or southern), with slopes averaging around 50 percent (Miller 1964, Scheldt 1969, Duncan 1975, Davis 1976). The shrubs characteristically grow in isolated patches but occasionally occur singly or in continuous extensive stands.

Curlleaf mountain mahogany grows at relatively high elevations throughout its range, but within any area of occurrence it is higher on southern than on northern exposures. It approaches or exceeds elevations of 3,000 m in the southern parts of its range (Brayton and Mooney 1966, Davis 1976), yet grows as low as 600 m in some areas of its northern range (Scheldt 1969). Most commonly it grows between 1,000 to 2,000 m (Duncan 1975, Miller 1964).

Soils are typically shallow (16 to 20 cm) sandy loams with low fertility, especially on the most xeric western and southern exposures. However, a few stands occur on loam, clay, and sandy clay loam sites (Davis 1976). The species appears to be indifferent to substrate because it occupies soils derived from limestone, dolomite, sandstone, quartzite, and granite and because the soils range from almost 6 to 8.5 in pH. Soluble salts are low (ranging between 92 and 550 ppm) in all the soils analyzed in Utah (Davis 1976). These and the previous soil values discussed correspond to those of Miller (1964), Brayton and Mooney (1966), Scheldt (1969), and Duncan (1975). The latter further found that in Montana the species occurs on soils that are low in phosphorus and only intermediate in potassium.

Youngberg and Hu (1972) reported in an Oregon study that curlleaf mountain mahogany produced root nodules capable of fixing nitrogen. They also determined that foliage nitrogen was highest in leaves from nodulated plants. Lepper and Fleschner (1977) further found that soils supporting limber pine-curlleaf mountain mahogany stands had higher percentages of total nitrogen than soils beneath similar limber pine (Pinus flexilis) stands without the curlleaf association. They concluded that the ability to fix nitrogen is a frequent characteristic in species adapted to extreme or pioneer habitats. If the capacity to fix nitrogen is universal in curlleaf mountain mahogany, it would help explain how the species can successfully occupy the infertile sites it so regularly inhabits.

Young trees have smooth bark and are grayish white in color, while older trees have characteristically rough, dark grey bark. Multiple stems are typical. Curlleaf mountain mahogany growth habit varies in Utah from a treelike form with about two stems per tree to shrublike with almost six stems per tree (Davis 1976). These varying growth forms were also observed in Idaho (Scheldt 1969), Wyoming (Miller 1964), and Montana (Duncan 1975). Davis (1976) also showed by regression analysis that the branching habit of curlleaf mountain mahogany was significantly correlated with percent soluble salts and percent sand in the soil. The relationship is even more evident in multiple step-wise regression. Soluble salts accounted for 52 of the total 66 percent variation, or 79 percent of the total variation accounted for by the regression. Therefore, with decreasing salts and increasing amounts of sand, the number of stems per tree increase. The relationship could be important in establishing curlleaf mountain mahogany in new areas. But without common garden studies, one cannot determine if the branching habit is an environmental adaptive or a fixed genetic response.

Average ages for curlleaf mountain mahogany in Utah ranged from 48 to 143 years with a mean of 85 years (Davis 1976). More than half of the individuals sampled fell between the ages of 56 to 109 years, with nearly one in 10 trees in a decadent condition (more than 25 percent of the crown dead). Oregon stands were on average younger than those in Utah (Dealy 1975), based on two regression equations devised to estimate the ages of the trees. One represented the moist sites and one the dry sites. When a mean was taken for the two regressions and compared with the regression for all sites in Utah, the estimated age of a stem 20.3 cm in diameter was 130 and 131 years, respectively. Although Utah stands are older on average, such remarkable similarity between regression equations suggests that curlleaf mountain mahogany growth is similar between the two areas. Ages reported for curlleaf mountain mahogany in Montana were much younger than those of Utah and Oregon, while those sites east of the Continental Divide were even younger (Duncan 1975). The oldest stands were from central and western Nevada, with ages ranging from 134 to 482 years and a mean of 352 years (Schultz et al. 1990).

In such stressful environments, selection favors growth habits that allocate most of the available resources to maintenance as opposed to growth and reproduction. Therefore, slow growth and longevity would be favored, minimizing the importance of seedling establishment in any given year. Almost 50 percent of the areas sampled in Utah had no trees in the less than 20-year age class (Davis 1976), indicating little or no reproduction on these sites. Reproduction on sites in Utah (Davis 1976) and Montana (Duncan 1975) ranged from 0 to around 600 seedlings per hectare. Such variation in reproduction indicates that a combination of environmental conditions is critical for germination and seedling establishment. Dealy (1975) found that seeds stratified in a moist medium at 4°C for 220 days produced almost 90 percent germination. These data suggest that a wet, somewhat mild winter is required for good stratification followed by an unusually wet spring and summer for good seedling germination and establishment. Scheldt and Tisdale (1970) observed that seedling mortality in the first summer was largely due to drought. They also showed that high winter mortality was due to grazing, mostly by rabbits. In addition, insect predation on mature seeds is common.

Another explanation for poor reproduction could be that good seed crops only occur every two to ten years (Plummer et al. 1968). Failure of seedling establishment can also be attributed to shade intolerance of seedlings, competition for water and other soil nutrients by mature trees, allelopathic response to curlleaf litter, and over-utilization of seedlings by a variety of wildlife species.

The lack of any one of the many combinations of critical factors needed for germination, establishment, and growth of young curlleaf mountain mahogany plants helps to explain why reproduction is so poor and inconsistent on most sites. However, such a low rate of reproduction in a species routinely attaining well over 100 years age may not be a serious problem.

Being a xerophyte, curlleaf mountain mahogany can be expected to have many inherent characteristics that help preserve water during droughty conditions. The most noticeable of these features is the leaves which have a thick cuticle, sunken stomata, thick covering of epidermal hairs, and revolute leaf margins. Other notable adaptations for survival include seedling root extension, shoot growth, and cool moist stratification, which ensure that germination occurs in early spring when it will have the best chance for survival. At the end of 120 days in an Oregon study, average root length was almost 1 m while shoot length was only a little over 2 cm (Dealy 1975). This is an example of the high degree of drought specialization characteristic of the species. Keeping the roots in contact with drying soils while limiting growth above ground assists in better seedling establishment within arid environments.

Curlleaf mountain mahogany is a highly palatable and preferred winter browse for both elk and deer (Smith 1952, Hoskins and Dalke 1955, Davis 1982[1]). It is also highly preferred even for summer use in some locations (Tueller 1979). Being evergreen, its nutritive value (about 12 percent protein) and digestibility ratings (around 50 percent) in the winter are high compared with most associated winter browse species. It is one of the few shrubs that exceed the protein requirements for wintering animals (Welch and McArthur 1979). For this reason, it merits special attention in big game management.

Where it is available, curlleaf mountain mahogany becomes an important winter browse species for mule deer in northeastern Utah (Richens 1967), and in eastern Oregon and Washington (Mitchell 1951). It would probably become more important as a winter browse species in many areas if it occurred at lower elevations within the lower latitudes (Smith and Hubbard 1954). It is especially critical for mountain goat survival in Idaho (Kuck 1980). In Utah, on one critical mountain goat wintering area, it is used by about 80 animals where it is basically the only browse available (personal observation).

Management Programs

A reconnaissance of curlleaf mountain mahogany winter range was completed by Ferguson and Klemmedson in 1965. They found most of the curlleaf ranges from southwestern Montana to southern Idaho to be in poor condition due to excessive use by wildlife and livestock. A summary of curlleaf mountain mahogany rehabilitation projects on the national forests of the Intermountain Region was completed in 1970 by Phillips. Both publications identified the major management problems in curlleaf communities as highlined, older, even-aged communities producing little accessible browse and little reproduction within the understory.

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[1] Davis, J.N. 1982. Unpublished data on file at the Shrub Sciences Laboratory, Provo, Utah.

Measures to increase available forage production from old, even-aged stands too tall to provide big game browse have long been a major research focus in the type. Pruning treatments were first tried in the late 1940's and early 1950's in Oregon. Some methods showed promise, but most failed and all were expensive (Lemons n.d.). Many managers have since investigated different pruning methods (Garrison 1953, Neff 1963, Thompson 1970, Shepherd 1971, Ormiston 1978, Austin and Urness 1980). Generally, they found that clipping over 50 percent of the limbs will increase twig production the following year. In some cases, twig production appeared to decrease after three or more years. Most researchers agree that pruning should be done during spring or early fall and then on mostly younger trees. Pruning done during the winter, especially on older age classes, causes death the next summer. Thompson (1970) further notes that reproduction was better under individual trees that had been pruned. The major drawbacks for this method of increasing browse production is that it is labor intensive; estimated costs run as high as $120 per hectare (Ormiston 1978).

Phillips (1970) describes one treatment that has shown promise in stand rehabilitation: bulldozed strips parallel and perpendicular to the slope to decrease competition and allow young mahogany plants to become established. The greatest benefit derived from the treatment was the spectacular growth of associated browse species, which produced available forage much faster and in greater quantities than curlleaf mountain mahogany.

The management of curlleaf mountain mahogany is made more difficult because it does not resprout after burning or chaining and it is troublesome to establish from seed. These characteristics do not leave many options for management manipulation. The major problem confronting the manager will be what to do with decadent communities of curlleaf with out-of-reach browse. There are no feasible quick fix methods. The pruning studies are an example of feasible but basically impractical treatments for increasing production.

The best overall approach, considered in the long term, would be to thin or take out old trees in small randomly placed and shaped openings. The thinning process could be done either by chaining or dozing, depending on the size and shape of the openings wanted within a stand. Release of associated shrub species in such openings would give some immediate relief to overused curlleaf mountain mahogany.

Where associated browse species are absent, thinning would create opportunities for young curlleaf seedlings to become established and younger age classes of curlleaf to become available. If other browse species are desired, seed dribblers (placed on both bulldozer tracks) could be used to plant shrub species that would establish and provide browse much sooner than the younger curlleaf plants. These species should not be planted in such a manner as to create problems for curlleaf establishment because the seedlings are not competitive with other plants. As with any revegetation project, reducing animal numbers (either big game or livestock) during specific times of the year may become necessary if the young plants are not able to become established.

TRUE MOUNTAIN MAHOGANY

True mountain mahogany is the second most widely distributed species of the genus Cercocarpus (Fig. 1). Its distribution appears to be centrally located in the foothills and mountains of Utah, Colorado, and Wyoming. The species also reaches into areas of South Dakota, Nebraska, Oklahoma, New Mexico, Arizona, and Nevada (Martin 1950, Medin 1960). The species is a deciduous shrub, or less commonly a small tree, usually one to four meters in height. It normally grows along ridges, bluffs, mountain slopes, and foothills at intermediate elevations between 1,000 and 3,000 m (Martin 1950, Medin 1960, Anderson 1974, Welsh et al. 1987). Although it more commonly grows at elevations between 1,500 to 2,200 m in Utah (Anderson 1974), the altitudinal range of curlleaf mountain mahogany and true mountain mahogany are generally separate, with the latter most often occurring on sites below those of the former. True mountain mahogany is typically associated with mountain brush, sagebrush, pinyon-juniper, aspen, and mixed conifer communities.

True mountain mahogany and curlleaf mountain mahogany diverge widely in Utah with respect to soil preference. Anderson (1974) found the most common textural class for true mountain mahogany was clay loam, with soil depth averaging almost twice that of curlleaf soils. It also occurred on soils that were generally more basic and more saline. True mountain mahogany has both root nodules for nitrogen fixation and mycorrhizae for phosphate uptake (Hoeppel and Wollum 1971). These associations undoubtedly help it survive on many of the infertile sites that it occupies, and that have been described as harsh and rocky, with shallow and undeveloped soils, especially on the warmer southern and westerly exposures (Brooks 1962). As with curlleaf mountain mahogany, all exposures are well represented, but the dominant exposure appears to become increasingly southern as elevation increases.

As a winter forage, it is often valued more highly than curlleaf mountain mahogany because it occupies lower elevations and is more available as winter browse even though it is deciduous and therefore has about half the protein of curlleaf (Kufeld et al. 1973). True mountain mahogany is rated as good to excellent browse for livestock and wildlife, especially deer (Plummer et al. 1968). Rominger et al. (1988) found it made up over 80 percent of the diet of Rocky Mountain bighorn sheep on one low elevation summer range in Colorado.

The overall management of true mountain mahogany is somewhat easier than that of curlleaf because more options are available for manipulating its productivity. First, because it is lower wildlife reach it more easily. Second, it grows much faster than curlleaf and will resprout following disturbance. True mountain mahogany stands in poor condition can often be readily rehabilitated. On large areas of such land, an economical method of treatment would be to aerially seed with selected grasses and forbs followed by one-way chaining. Chaining on the contour should be done if the slopes are not too steep and downhill if they are. This would provide good seedbed preparation for the establishment of needed grasses and forbs while thinning out the older mahogany plants and decadent portions of the younger plants. The degree of thinning can be adjusted by the weight and smoothness of the chain being used and the distance between the bulldozers. If necessary, associated shrub species could be seeded by dribblers mounted above the bulldozer tracks.

LITTLE LEAF MOUNTAIN MAHOGANY

Little leaf mountain mahogany can be found throughout most of Utah (Welsh et al. 1987), sporadically through Nevada, in the eastern and southern half of California, northernmost Arizona, and extreme western Colorado (Fig. 1). This narrow-leafed, intricately branched evergreen shrub (0.5 to 3 m in height) is ecologically a bit of a mystery because of its restricted habitat. Holmgren (1987) described it best as growing in shallow soils or in cracks and crevices of rock outcrops where few other plants can be found. Because it is so commonly found growing on rock faces and cliffs, little is known about its soil relations. It appears to thrive on rimrock, cliffs, and rocky dry slopes within desert shrub, pinyon-juniper, and mountain brush communities from 900 m elevation in Arizona to almost 3,000 m in California (Kearney and Peebles 1942, Harrington 1964, Munz 1973).

Basically, little leaf mountain mahogany occurs in one of two basic habitats: steep rocky canyon surfaces, or pinyon-juniper woodlands and desert shrubs identified with poorly developed soils. Brayton and Mooney (1966) described the canyon type in southeastern California, where it is apparently restricted to steep limestone sites with little soil development. The "type collection" for Utah (Martin 1950) was collected on a similar site in American Fork Canyon where it occurs almost exclusively on steep limestone canyon slopes. Of special interest is a nearby canyon formed in granite; curlleaf mountain mahogany is present but little leaf does not occur in the steep granite canyons. Brayton and Mooney (1966) further found that little leaf occurred from 1,800 to 3,000 m while curlleaf mountain mahogany was restricted to the higher elevations (2,700 to 3,200 m) and seemed indifferent to substrate. Rock cover on the little leaf mountain mahogany sites exceeded 90 percent with minimal soils being slightly alkaline (8 to 8.5 pH).

Fairchild and Brotherson (1980) provided basic ecological information for the desert shrub type. They found it to be one of six species important in the pinyon-juniper understory of northeastern Arizona. Little leaf mountain mahogany appeared as a pioneering species, functioning in soil development and establishment of islands of vegetation within the slickrock areas. Growing under these harsh conditions, one would have to assume that it would have similar characteristics to that of the other two mountain mahoganies with the ability to fix nitrogen by root nodulation. Again, Fairchild and Brotherson (1980) found the greatest amounts of rock associated with this species, with soils averaging about 17 cm in depth and over 80 percent sand. Soil pH was neutral to slightly alkaline. Both studies generally support the basic axiom about the species distribution within its range of occurrence: within the Colorado Plateau, it generally occurs on substrates of sandstone, while within the Great Basin it is common on substrates of limestone.

No studies compare animal preference for little leaf mountain mahogany with other browse species. It is probable that little leaf has nutritional characteristics similar to curlleaf mountain mahogany because of its evergreen habit. The shrub always appears to be utilized when available. Because of its restrictive habitat, it could become an important browse species for Rocky Mountain goats, desert big horn sheep, and Rocky Mountain big horn sheep, which already use it in the Flaming Gorge area. In some areas where it is more exploitable, deer and other wildlife appear to use it readily. Because of its limited and restrictive habitat, little leaf mountain mahogany has not been manipulated by seeding, chaining, and burning treatments, or by other commonly used management options.

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TAXONOMY AND EVOLUTION OF *CERCOCARPUS* IN THE WESTERN UNITED STATES

Howard C. Stutz

ABSTRACT: Four taxa of mountain mahogany (Cercocarpus) occur in the Intermountain West of the United States. True mountain mahogany (C. montanus), the only deciduous species, apparently arrived from the south. Two varieties of curlleaf mountain mahogany arrived from the north and northwest. C. ledifolius var ledifolius has leathery leaves with inrolled edges that are densely pubescent ventrally. The leathery leaves of C. ledifolius var intermontanus are spatulate and glabrous. Little leaf mountain mahogany (C. intricatus), primarily endemic to Utah, was derived directly from C. ledifolius var ledifolius. Upon contact, intertaxon hybrids form between all of the taxa but only those that involve C. ledifolius var ledifolius as one of the parents produce hybrids with significant segregant progeny.

TAXONOMY

The genus Cercocarpus is endemic to Mexico and the western United States. It was originally assigned to the section Sanguisorbeae Juss in the family Rosaceae (H.B.K. 1823). It was later placed in the subtribe Cercocarpeae of the tribe Dryadeae (Torrey and Gray 1840). Facke (in Engler and Prantl 1889) raised the subtribe Cercocarpeae to the status of tribe and included in it the genera Adenostoma, Cercocarpus, Coleogyne, Purshia and Chamaebatia. Rydberg (1913) narrowed the tribe Cercocarpeae to contain only Cercocarpus. All subsequent treatments have retained this designation (Martin 1950, Pyrah 1964, Henrickson 1987).

Cercocarpus is distinguished by a collage of characteristics setting it apart, distinctly, from all other rosaceous genera. These include perigynous flowers with no petals, one-celled ovaries enclosed by a tubular persistent calyx, and hairy styles forming elongated persistent tails on the

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achenes. The wood is very hard, for which Cercocarpus received the common name "mountain mahogany" from early Mormon settlers. However, because the name "mahogany" has already been given to Swietenia mahogani Jacq., the tree from which mahogany lumber is derived, "cercocarpus" has been assigned as the approved common name for Cercocarpus (Hayes and Garrison 1960).

Four taxa of Cercocarpus are common in the western United States: C. ledifolius Nutt. var ledifolius, C. ledifolius var intermontanus N. Holmgren, C. intricatus S. Wats and C. montanus Raf. var montanus Martin (Fig. 1).

Until recently C. ledifolius var ledifolius has been referred to as C. ledifolius var intercedens Schneider or as C. hypoleucus Rydb. However, as pointed out by Holmgren (1987), this is the taxon that was originally described by Nuttall as C. ledifolius and differs significantly from the broader-leafed form commonly referred to as C. ledifolius (Table 1). Appropriately, Holmgren therefore designated the originally described taxon as C. ledifolius var ledifolius and the other common form as C. ledifolius var intermontanus.

C. ledifolius var ledifolius has narrower, more strongly involute leaves than C. ledifolius var intermontanus. Also its leaves differ from leaves of C. ledifolius var intermontanus in being densely pubescent ventrally. Its habit is more shrubby and its distribution more northerly than var intermontanus (Table 1, Fig. 2a, 2b). In northern Wyoming, northern Idaho and southern Montana it is the only form of Cercocarpus present.

In many places throughout its northern distribution, C. ledifolius var ledifolius is very abundant, particularly on the leeward side of ravines where accumulations of snow apparently favor its success. Dense thickets are also often conspicuous on north and east-facing slopes, apparently benefitting from reduced transpiration on these exposures. Most individual plants grow to approximately 1 meter in diameter and 1 meter in height. However, north of Sheridan, Wyoming, some individual plants are more than 4 meters in diameter and 2 meters in height. In Utah and Nevada individual plants are typically more erect and less dense than those in the northern populations. Extensive populations are common in the Uintah mountains of Utah but are scarce in the other mountain ranges of the area. Small populations have been found as far south as Ely and Eureka, Nevada.

C. ledifolius var intermontanus is likewise common in Utah and northern Nevada, sometimes growing intermixed with C. ledifolious var ledifolius. Its distributional range extends mostly westward and northwestward into northern California and southern Oregon (Fig. 2b). Var intermontanus usually grows in dense groves, often as small trees up to twenty feet in height, with boles up to twelve inches in diameter. Its leaves are broadly elliptic and glabrous (Fig. 1).

Cercocarpus intricatus has tiny (1 cm x 2 mm), strongly involute leaves that are densely pubescent ventrally (Fig. 1). In

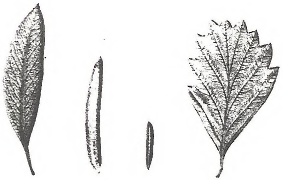

Figure 1. Leaves of the four *Cercocarpus* taxa common to western United States. From left to right: *C. ledifolius* var. *intermontanus*, *C. ledifolius* var *ledifolius*, *C. intricatus*, *C. montanus*.

Table 1. Characteristics of the four *Cercocarpus* taxa common to the Intermountain West of the United States.

Characteristic	Taxa[a] *led led*	 *led interm*	 *montanus*	 *intricatus*
habit	large shrubs	small trees	shrubs	small shrubs
leaf deciduosity	evergreen	evergreen	deciduous	evergreen
leaf involution	strong	slight	none	very strong
leaf pubescence	abundant	none	none	abundant
anther hairiness	none	none	high	none
distribution	MT to UT	No. CA, So. OR to UT	Central WY through UT	UT only
fertility of hybrids with *montanus*	high	low	---	zero

[a] *led led* = *C. ledifolius* var *ledifolius*, *led interm* = *C. ledifolius* var *intermontanus*.

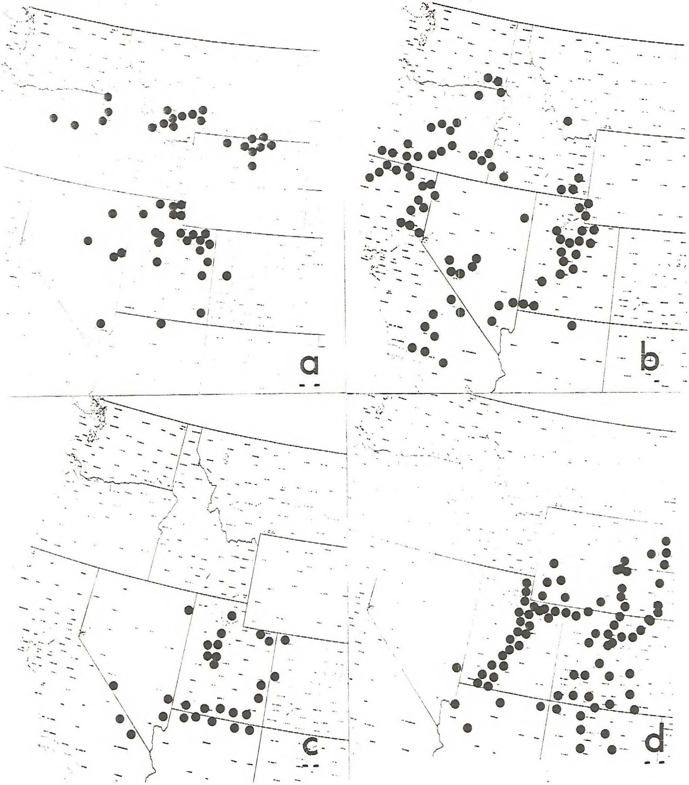

Figure 2. Distribution maps of Cercocarpus taxa in western United States. a. C. ledifolius var ledifolius. b. C. ledifolius var intermontanus. c. C. intricatus. d. C. montanus (adapted from Martin 1950).

some populations the dorsal side of the leaves are dull and finely puberulent, in others they are shiny and glabrous. The plants are small-statured shrubs, usually about 1 to 1 1/2 meters in diameter and 1 1/2 to 2 meters in height. They usually grow in crevices of rocky outcrops. In distribution, C. intricatus is confined almost entirely to the state of Utah and the borders of contiguous states (Fig. 2c). Collections reported from elsewhere are apparently of C. ledifolius var ledifolius, not C. intricatus.

C. montanus is the only species of Cercocarpus in the western United States with deciduous leaves. It is also the only one with hairy anthers. Several varieties of C. montanus have been described from California and Mexico (Martin 1950, Henrickson 1987) but the only one common in the intermountain area is C. montanus var montanus. Its distribution is from central Wyoming and South Dakota to Oklahoma, Arizona and New Mexico and westward throughout Utah and Nevada to eastern California (Fig. 2d). In Wyoming it usually forms pure dense stands on steep north and east slopes. In Utah it is often associated with other shrubs such as chokecherry (Prunus virginiana), serviceberry (Amelanchier alnifolia), scrub oak (Quercus gambellii) and squawberry (Rhus trilobata). Individual plants are usually about 1 meter in diameter and 1 1/2 meters tall but are often much bushier (wider and denser) in response to livestock and wildlife grazing.

NATURAL HYBRIDIZATION

Throughout their distributional ranges, each of the four Cercocarpus taxa described above comes into contact with each of the others, producing intertaxon hybrids. In Utah, they all come together and all possible hybrid combinations are formed.

Hybrids between C. ledifolius intermontanus and C. montanus are fairly common and are easily recognized because they are intermediate between both parents in stature and in leaf characteristics. Their large tree-like form, towering above the much shorter C. montanus plants with which they grow, make them particularly conspicuous. Their leaves are coarsely toothed at the apex like leaves of C. montanus but are coriaceous and spatulate like leaves of variety intermontanus (Fig. 3). In wintertime they remain attached while all the surrounding C. montanus leaves abscise. Hybrid leaves are often amusingly green at the base, brown at the apex.

Because the hybrids always occur in stands of C. montanus they apparently result only when C. montanus is the female parent. C. ledifolius var intermontanus normally flowers at least two weeks earlier than C. montanus so cannot receive C. montanus pollen. However, pollen from C. ledifolius var intermontanus is readily available for pollinating C. montanus flowers. As shown in Table 2, Cercocarpus pollen remains viable for several days so it could be available when C. montanus plants come into flower

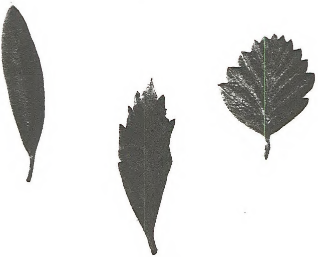

Figure 3. Leaves of *Cercocarpus ledifolius* var *intermontanus* (left), *C. montanus* (right), and an F_1 hybrid between them.

Table 2. Duration of pollen viability[a] for *Cercocarpus montanus* and *C. ledifolius* var *intermontanus* (modified from Pyrah 1964).

	montanus			var *intermontanus*		
Age	germination			germination		
days	N	#	%	N	#	%
1	362	278	76.8	374	152	40.7
2	331	91	27.5	---	---	---
5	305	65	21.3	222	42	18.9
10	332	82	24.7	308	38	12.3
14	381	81	21.2	228	20	8.8

[a] Pollen was germinated on sterile nutrient agar.

even though it were produced earlier. Also late-flowering plants could furnish fresh pollen.

Although C. montanus x C. ledifolius var intermontanus hybrids are common, they apparently rarely leave offspring. Part of the reason for this could be the disjunct flowering times but mostly it appears to be the result of genetic incompatibility. As shown in Table 3, pollen fertility in these hybrids is low. Also, although fruits are produced, they are apparently completely sterile (Table 4).

Only a few hybrids have been found from C. montanus x C. ledifolius var ledifolius parents. This is probably because the parents do not often grow together and also because the hybrids are less conspicuous. Because the stature of C. ledifolius var ledifolius is not much greater than that of C. montanus, hybrids between them are not easily detected by stature alone as are the hybrids between C. montanus and C. ledifolius var intermontanus. In wintertime they are more easily detected because their evergreen habit make them conspicuous when growing among deciduous C. montanus plants.

In contrast to C. montanus x C. ledifolius var intermontanus hybrids, C. montanus x C. ledifolius var ledifolius hybrids appear to be quite fertile (Table 3). Segregating backcross progeny from these hybrids are abundant and can be identified by their varying leaf characteristics as well as by the degree of anther-hairiness (Table 5).

In contact zones between C. ledifolius var ledifolius and C. ledifolius var intermontanus, hybridization appears to be so abundant that total integration results. This is true also for C. ledifolius var ledifolius and C. intricatus. In some populations including hybrids it becomes very difficult to determine whether a plant is C. intricatus or C. ledifolius var ledifolius.

Hybrids between C. intricatus and C. ledifolius var intermontanus are common in some zones of contact between these two species but are strikingly absent elsewhere, suggesting the presence of genetic differences within the parents.

Hybrids between C. intricatus and C. montanus (Fig. 4), however, are rare and when they do occur they appear to be completely sterile. In most cases hybrids do not even form flowers.

EVOLUTION

The geographical and ecological distributions, morphological attributes, and intertaxon hybridization performance permit an interpretation of the evolutionary history of Cercocarpus. Apparently each of the four taxa has come into Utah by a separate route. C. montanus var montanus almost certainly arrived from the south. Its nearest relatives appear to be the evergreen taxon C. montanus var paucidentatus (S. Wats) Martin, common in the mountains of Arizona, New Mexico, Texas and Mexico; C. montanus var argenteus (Rydb) Martin from New Mexico and Texas; and the Mexican species C. mexicanus Henrickson, C. rzedowski Henrickson and C. fothergilloides Kunth.

[a] Pollen was germinated on sterile nutrient agar.

Table 3. Pollen fertility of *Cercocarpus* taxa[a] (modified from Pyrah 1964).

Taxon	germination		
	N	#	%
montanus	362	278	6.8
mont X *led* *led*	7466	1423	19.1
mont X *led* *interm*	3033	180	5.9

[a] Fresh pollen was sown on nutrient agar at room temperature.

Table 4. Percent seed germination[a] for seeds of *Cercocarpus* *montanus*, *C.* *ledifolius* var *intermontanus* and hybrids between them (modified from Pyrah 1964).

Taxon	germination		
	N	#	%
montanus	875	92	10.5
var *intermontanus*	605	40	6.6
hybrids	1983	0	0

[a] The seeds were scarified 5 minutes in concentrated sulfuric acid, then sown on moistened filter paper at room temperature.

Table 5. Degree of anther hairiness in the hybrids[a] Cercocarpus montanus x C. ledifolius var ledifolius and C. montanus x C. ledifolius var intermontanus.

Degree of anther hairiness[b]	mont x led led	mont x led interm
	-----------# of plants-----------	
4	3	0
3	5	6
2	8	5
1	10	5
0	3	1

[a] "Hybrids" were those plants showing intermediate leaf characteristics. Some may have been F_1 hybrids, some may have been backcross progeny.

[b] Degree of hairiness was scored as follows:
4 = very hairy as in C. montanus, 3 = hairy, 2 = slightly hairy, 1 = occasional hair, 0 = no hairs as in C. ledifolius.

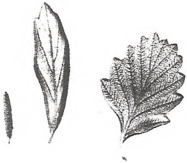

Figure 4. Leaves of Cercocarpus intricatus (left), C. montanus (right) and an F_1 hybrid between them.

C. ledifolius var ledifolius apparently came into Utah from the north but has become somewhat modified from its northern progenitors. The northern plants are much bushier and denser in habit than the southern plants. This may be a result of more severe grazing by herbivores in the northern populations or, more likely, the southern forms are genetically modified.

The southern form of C. ledifolius var ledifolius has apparently produced, by gradual genetic assimilation, Cercocarpus intricatus. The evolutionary process that produced C. intricatus is still proceeding. Intermediate steps are abundant and widespread throughout Utah, so much so that many herbarium collections of C. ledifolius var ledifolius are mislabelled C. intricatus. C. intricatus differs phenotypically from C. ledifolius var ledifolius only in being smaller statured, more drought tolerant and having fewer stamens (10-15 versus 15-20) and shorter tails on the fruits (1-2 cm versus 3-6 cm). Consequently errors in identification are to be expected.

In the acquisition of genetic changes that now separate C. intricatus from C. ledifolius var ledifolius, reproductive barriers have been included, which prevents C. intricatus from exchanging genes with C. montanus. As described above, C. ledifolius var ledifolius hybridizes freely with C. montanus in areas of contact, producing fertile hybrids and a wide array of segregating progeny. But C. intricatus x C. montanus hybrids are extremely rare and those that have been found appear to be completely sterile, usually failing to even produce flowers.

C. ledifolius var intermontanus appears to have come to Utah from northern California and southern Oregon. Upon contact, it hybridizes rather freely with each of the other species, suggesting the presence of few reproductive barriers and hence rather recent contact.

In summary, the four taxa of Cercocarpus now growing in the Intermountain West are:

1. C. montanus, the only deciduous species, apparently arrived from the south.

2. C. ledifolius var ledifolius arrived from the north. Northern populations are bushier than southern populations. Its leathery leaves with inrolled edges are densely pubescent ventrally.

3. C. ledifolius var intermontanus arrived from the northwest. It has spatulate, glabrous, leathery leaves. This is the taxon that has been commonly referred to as "leather-leaf" or "curl-leaf" mahogany.

4. C. intricatus, primarily endemic to Utah, was derived directly from C. ledifolius var ledifolius.

Upon contact, intertaxon hybrids form between all of the taxa but only those that involve C. ledifolius var ledifolius as one of the parents produce hybrids with significant segregant progeny (Table 6). Because of its bushy habit, cold and drought tolerance, and apparently excellent forage values, many useful selections, both natural and designed, can be expected from its hybrid products.

Table 6. Summary of natural hybridization in Cercocarpus.

Parents[a]	Opportunity for hybridization	Abundance of F_1 hybrids in contact zones	Progeny from F_1 hybrids
led led x led interm	low	high	abundant
led led x intricatus	high	high	abundant
led led x montanus	low	high	abundant
led interm x intricatus	moderate	moderate	moderate
led interm x montanus	moderate	high	few
intricatus x montanus	moderate	low	none

[a] led led = C. ledifolius var ledifolius, led interm = C. ledifolius var intermontanus.

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SEED DORMANCY IN TWO SPECIES OF MOUNTAIN MAHOGANY

(*CERCOCARPUS LEDIFOLIUS* AND *CERCOCARPUS MONTANUS*)

Stanley G. Kitchen and Susan E. Meyer

ABSTRACT: Although seed dormancy in Cercocarpus ledifolius (curlleaf mountain mahogany) and Cercocarpus montanus (true mountain mahogany) has been investigated by several authors, considerable confusion remains concerning the nature of seed dormancy and the chilling requirements needed to break dormancy for these two species. This study was conducted to determine seed dormancy characteristics for collections of both species taken from a broad geographic and elevational distribution. Dormancy breaking treatments were applied to freshly harvested seeds from six C. ledifolius and nine C. montanus populations. Mean germination of untreated seeds was 0.5 and 15%, respectively. Germination during 10 weeks of moist chilling (1°C) ranged from 11 to 52% for the C. ledifolius collections and from 1 to 85% for the C. montanus collections. Mean germination for all collections of both species at 16 weeks was 95%. In a second experiment, the effect of the duration of moist chilling (1°C) on subsequent germination at 15°C was determined. The minimum period of moist chilling required for complete germination ranged from 6 to 12 weeks for the C. ledifolius collections and from 4 to 12 weeks for the C. montanus collections. Germination responses to chilling and winter precipitation at the collection site were significantly correlated, suggesting that snowpack is important in determining the length of chilling treatment required to break seed dormancy. Establishment success of these species may be improved by planting locally collected seed that should be better matched to environmental conditions at the seeding site.

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INTRODUCTION

Two species of mountain mahogany (*Cercocarpus* H.B.K.) are recognized as major browse species on winter ranges in the Intermountain West. *Cercocarpus ledifolius* Nutt. (curlleaf mountain mahogany) is evergreen and highly favored by mule deer. *Cercocarpus montanus* Raf. (true mountain mahogany), though deciduous, is less tree-like and thus generally more available to deer than *C. ledifolius*. It is a major component of the winter diet of mule deer and other big game species (Plummer et al. 1968).

Both species have been included in revegetation programs using direct seeding. Large quantities of seeds can be harvested during good production years. The seeds of both species are long-lived in storage (Stevens et al. 1981), permitting carryover of seed reserves for use in poor production years. Mountain mahogany seeds are relatively expensive compared to those of many other native shrub species (Ron Stevenson, personal communication). Consequently, efforts are warranted to improve establishment success through better understanding of the germination requirements of these species.

Stand establishment has been particularly difficult for *C. ledifolius*. Some have attributed this to excessive seed dormancy (Liacos and Nord 1961, Young et al. 1978). Some research has focused on developing treatments (i.e., thiourea, hydrogen peroxide, and scarification with sulfuric acid) that reduce or eliminate seed dormancy enabling the seed to be sown in the spring (Young et al. 1978, Stidham et al. 1980). However this approach is impractical for field application considering the unpredictability of spring moisture.

A number of papers have dealt with the response of *C. ledifolius* to moist chilling (stratification). Young et al. (1978) reported no germination response to 12 weeks of chilling using seed collected in Nevada. Similarly, Stidham et al. (1980) had unsatisfactory results after 10 weeks of chilling (seed origin unknown). Conversely, Heit (1970) claimed that four weeks of chilling was adequate for good germination. This conclusion was based on eight years of work with several collections. Using an Oregon collection, Dealy (1975) reported only 20% germination after almost nine weeks of chilling (60 days). He demonstrated that *C. ledifolius* seeds could germinate during chilling (4°C), reporting 80% germination in 19 weeks (135 days) of treatment.

Reports of natural emergence following good seed production years are also inconsistent. Young et al. (1978) observed no natural recruitment in "hundreds" of mature stands in the Great Basin, but Scheldt and Tisdale (1970) observed good emergence (mean of 1.9 seedlings/ square foot) on most of 17 Idaho sites during a single spring. They attributed the high levels of seedling mortality to summer drought and fall/winter herbivory. Unpredictable postemergence factors (i.e., frost, drought, competition, herbivory) must play a major role in determining natural recruitment.

Cercocarpus montanus seeds are generally believed to be less dormant than those of C. ledifolius. This is generally supported in the literature, although conflicting results are also reported. Moore (1963) found that C. montanus seeds from near Boulder, Colorado failed to respond to 52 days of chilling. Though agreeing that this species is less dormant than C. ledifolius, Heit (1970) claimed that chilling did not reduce its dormancy. Using seed from various New Mexico collections, Piatt (1973, 1976) and Springfield (1971) determined that 28 to 42 days of chilling was sufficient to break dormancy in most seeds.

Variation in experimental procedures such as chilling temperature, germination temperature, moisture control, seed age, and storage conditions probably account for much of the discrepancy in these results. In addition, some researchers failed to account for the effect of nonviable seeds. The significance of this becomes apparent when one realizes that fill in some lots is below 50%. Finally, one should not assume that dormancy for seeds taken from sites with considerable variation in winter precipitation and temperature patterns would be similar. Attempts to compare seed dormancy among several geographically widespread collections have not been reported for these two species.

The objectives of our work were to determine for several collections of both species 1) the rate of germination during chilling (1°C), and 2) total germination at a moderate temperature (15°C) following various chilling periods (0 to 12 weeks). We also considered the possible correlation between these two measures of seed dormancy and mean winter precipitation (an estimate of snowpack) at the several collection sites. The concept of climate-driven variation in chilling requirements has been demonstrated in other Rosaceous genera (Westwood and Bjornstad 1968, Barclay and Crawford 1984).

MATERIALS AND METHODS

Seeds were harvested from six C. ledifolius and nine C. montanus populations over a 6-week period during the summer of 1987 (Table 1). Each collection was cleaned of styles and inert matter using standard techniques and stored in envelopes at approximately 20°C (room temperature) prior to counting for each experiment. Seeds for each experiment were hand-selected to minimize the frequency of nonviable seeds.

We used a completely randomized design in both experiments, including four replications of 25 seeds each for each treatment. Seeds were placed in 100 mm plastic petri dishes between two standard germination blotters. Blotters were moistened to saturation with tap water and additional water was added as

Table 1.--County, state, altitude of collection site, and collection dates for seed lots used in this study.

Species Collection	County	State	Altitude	Collection Date
Cercocarpus montanus			Meters	1987
Lake Mountain	Utah	Utah	1890	7/17
Talmage	Duchesne	Utah	1920	7/22
Starvation	Duchesne	Utah	1800	7/23
Burr Trail	Garfield	Utah	2040	7/24
Kolob Road	Washington	Utah	2280	7/26
Spanish Fork Canyon	Utah	Utah	2100	7/28
Indian Canyon	Carbon	Utah	1860	7/28
Fort Collins	Larimer	Colorado	1650	8/05
Poudre Canyon	Larimer	Colorado	1950	9/01
Cercocarpus ledifolius				
Cedar Canyon	Iron	Utah	1980	7/26
City of Rocks	Cassia	Idaho	1860	8/01
Lake Mountain	Utah	Utah	2160	8/05
Lamoille Canyon	Elko	Nevada	2010	8/10
Salt Creek Canyon	Utah	Utah	2460	8/29
Salina Canyon	Sevier	Utah	2340	8/--

necessary. Dishes were randomly arranged in cardboard boxes enclosed in plastic bags to help retain moisture and to facilitate handling. Seeds with radicles at least five mm in length were considered germinated.

Experiment I

In the first experiment, germination rate at near-freezing temperature (1°C) was determined for each collection. Mean seed age was 60 days at the start of chilling. Germination percentages were determined weekly for 16 weeks. At 16 weeks the box containing the seeds was moved to a chamber set at 15°C for two weeks after which final germination counts were taken. The viability of ungerminated seeds was determined by a cut test. Seeds with discolored and decomposed embryos or no embryo at all were classified as nonviable. Germination percentages were adjusted to indicate percentage of total viable seed, thus minimizing the variability caused by differences in viability among collections.

Experiment II

In the second experiment, the effectiveness of various periods of moist chilling in breaking dormancy was measured. Chilling periods were 0, 2, 4, 6, 8, and 12 weeks for the C. montanus collections and 0, 4, 6, 8, 10, and 12 weeks for the C. ledifolius collections. The germination period was 28 days at 15°C.

The highest germination percentage for 14 of the 15 collections in this experiment was not significantly different from the estimate of total viable seed used in Experiment I. For this reason we present the results using the highest germination percentage as an estimate of total viable seed.

Germination percentages were arcsine transformed for statistical analysis. We analyzed results by collection and species using analysis of variance. Significant differences among treatments were determined using the Student-Neuman-Keuls (SNK) method.

The hypothesis that germination response to moist chilling is correlated with the duration of snowpack at the collection site was tested using regression analysis. We used an estimate of mean winter (December through February) precipitation as an indicator of duration of snowpack. This value was estimated using data from nearby weather stations and annual precipitation maps (Water Information Center 1974).

RESULTS

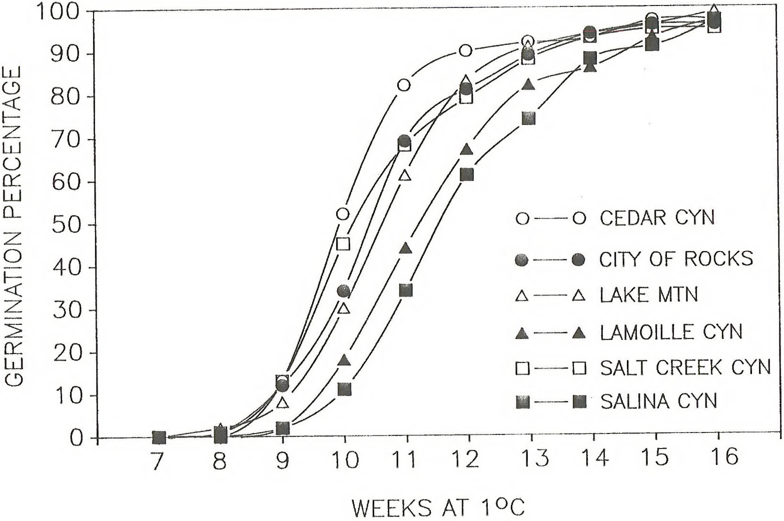
Experiment I

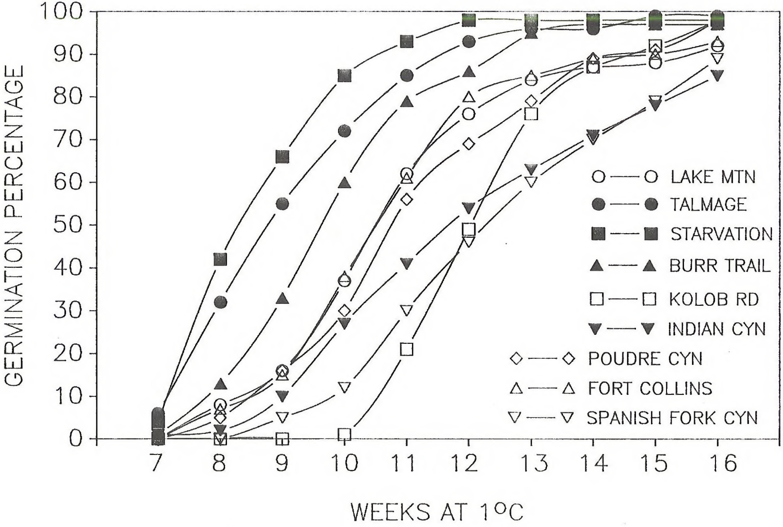
The treatment was sufficient to break dormancy in all seeds. Seed viability ranged from 80 to 99% for the C. ledifolius collections and from 71 to 95% for the C. montanus collections. Total germination was equal to percentage viable seed for each collection.

Germination at 1°C started at seven weeks for the C. montanus collections and at eight weeks for the C. ledifolius collections (Figures 1 and 2). Germination at 16 weeks was essentially complete for both species, ranging from 85 to 99% for C. montanus and from 95 to 99% for C. ledifolius. Between-collection variability in germination initiation and germination rate was greater among the C. montanus collections than the C. ledifolius collections. Among-collection differences in germination percentages were widest at 10 weeks. At this point germination ranged from 1 to 85% for the C. montanus collections and from 11 to 52% for the C. ledifolius collections. Mean germination for the C. montanus collections was slightly higher than that of the C. ledifolius collections at 8, 9, and 10 weeks of chilling (Figure 3). The mean germination percentages of both species were nearly identical at week 10 of chilling.

Experiment II

Mean germination for the nine C. montanus collections was 15% in the no-chill control (Table 2). After two weeks of chilling, the Fort Collins and Poudre Canyon collections had significant increases in germination percentage compared to the control. The mean increase for these two collections was 46%. Eight of nine collections had significant increases after four weeks of chilling compared to the control, with a 55% range in germination. While germination percentages for five of the nine


GERMINATION PERCENTAGE
0
10
20
30
40
50
60
70
80
90
100
7
8
9
10
11
12
13
14
15
16
WEEKS AT 1°C
○—○ CEDAR CYN
●—● CITY OF ROCKS
△—△ LAKE MTN
▲—▲ LAMOILLE CYN
□—□ SALT CREEK CYN
■—■ SALINA CYN


100
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GERMINATION PERCENTAGE
7
8
9
10
11
12
13
14
15
16
WEEKS AT 1°C
○—○ LAKE MTN
●—● TALMAGE
■—■ STARVATION
▲—▲ BURR TRAIL
□—□ KOLOB RD
▼—▼ INDIAN CYN
◇—◇ POUDRE CYN
△—△ FORT COLLINS
▽—▽ SPANISH FORK CYN

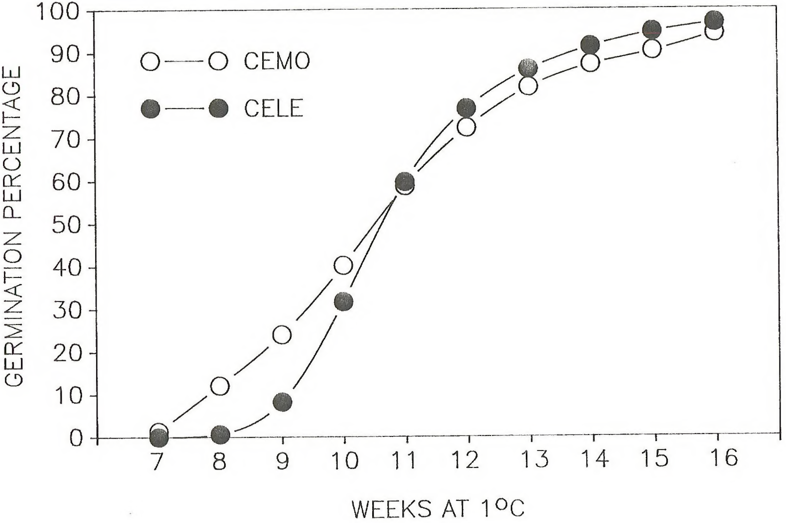

100
90
80
70
60
50
40
30
20
10
0
GERMINATION PERCENTAGE
○—○ CEMO
●—● CELE
7
8
9
10
11
12
13
14
15
16
WEEKS AT 1°C

Table 2. Germination response of *Cercocarpus montanus* at 15°C following various chilling treatments at 1°C. Germination percentages are given as a percentage of the estimate of total viable seed for each collection.

	Weeks of Chilling					
Collection	0	2	4	6	8	12
	---------germination percentage[a]----------					
Lake Mountain	21c	15c	33c	69b	81b	100a
Talmage	17c	24c	55b	93a	100a	98a
Starvation	15c	19c	73b	88a	100a	98a
Burr Trail	21d	28d	64c	87b	90ab	100a
Kolob Road	6d	5d	33c	67b	91a	100a
Spanish Fork Canyon	14d	23d	49c	78b	80b	100a
Indian Canyon	10c	24c	49b	87a	77a	100a
Fort Collins	15d	58c	69bc	86ab	88ab	100a
Poudre Canyon	12c	61b	88a	96a	100a	87a
Means	14.6f	28.6e	57.0d	83.4c	89.7b	98.1a

[a] Within a collection, means followed by the same letter are not significantly different at the $p<0.05$ level.

collections were not significantly different than estimates of total viable seed after six weeks of chilling, two collections (Lake Mountain and Spanish Fork Canyon) required 12 weeks of chilling for complete germination.

Only one of the six *C. ledifolius* collections (Salt Creek Canyon) had any germination (3%) in the unchilled control (Table 3). All collections responded to four weeks of chilling with a range of 51% in germination. Although germination percentages not significantly different from the estimate of total viable seed were observed for two collections (Cedar Canyon and Salt Creek Canyon) after six weeks of chilling, and for four collections after eight weeks of chilling, one collection (Lamoille Canyon) required 12 weeks of chilling for complete germination.

DISCUSSION

Laboratory experiments such as those conducted in this work are not simulations of the complex conditions that a seed might undergo in the soil during winter months. However, they do make it easier to establish cause and effect between specific environmental stimuli and changes in seed dormancy.

The seeds of these collections of *C. montanus* were apparently less dormant than those of the *C. ledifolius* collections as measured by germination response after zero and four weeks of chilling (Tables 2 and 3).

Table 3. Germination response of Cercocarpus ledifolius at 15°C following various chilling treatments at 1°C. Germination percentages are given as a percentage of the estimate of total viable seed for each collection.

	Weeks of Chilling					
Collection	0	4	6	8	10	12
	germination percentage[a]					
Cedar Canyon	0c	59b	96a	100a	96a	96a
City of Rocks	0d	51c	83b	92ab	100a	94ab
Lake Mountain	0e	17d	79c	90b	99a	100a
Lamoille Canyon	0e	8d	53c	81b	91b	100a
Salt Creek Canyon	3c	41b	82a	94a	100a	98a
Salina Canyon	0d	17c	65b	93a	90a	100a
Means	.5e	32.2d	76.3c	91.7b	96.0ab	98.0a

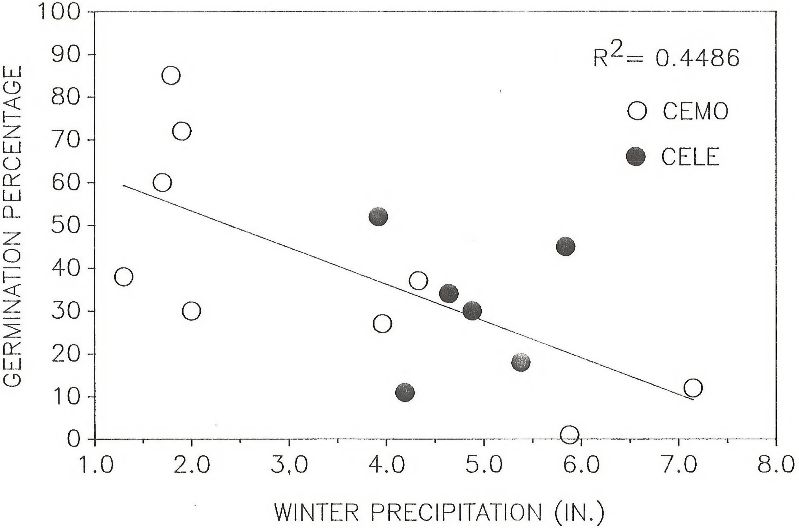
[a]Within a collection, means followed by the same letter are not significantly different at the $p<0.05$ level.

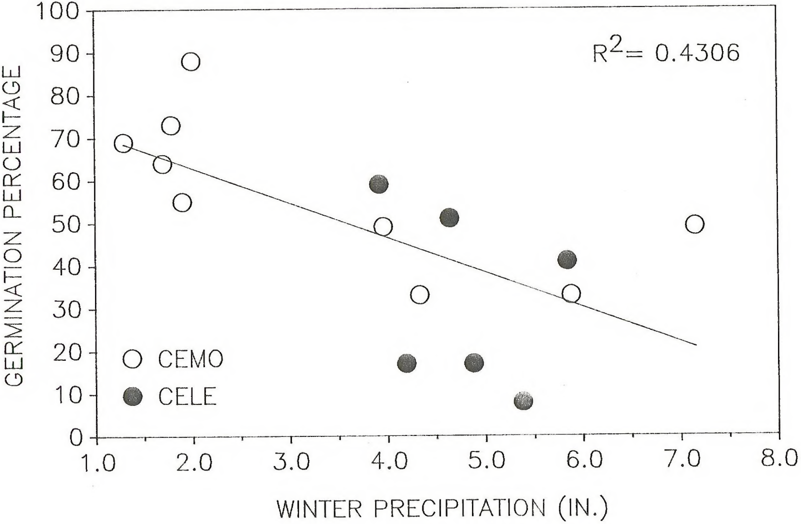
There was essentially no difference between the species after chilling periods of six weeks or longer. Similarly, there was little notable difference in mean germination rates at 1°C (Figure 3). Thus, based on these data, there appear to be only minor differences in chilling requirements between these two species.

However, our data show that considerable differences in dormancy do exist among the collections of each species (Tables 2 and 3 and Figures 1 and 2). Much of this variability may be explained by a correlation of chilling requirement with some relevant environmental factor.

Effective moist chilling under field conditions is apparently limited to periods when snowpack is adequate to allow soil surface temperatures to rise just above freezing. As stated previously, the duration of such conditions should be at least loosely related to mean winter precipitation. Mean winter precipitation at the collection site was significantly correlated with germination percentage at 10 weeks of chilling (Figure 4) and germination percentage after four weeks of chilling (Figure 5) for both species combined. The correlation was not significant for the C. ledifolius collections alone, however. This may be due in part to the narrower range in winter precipitation for the C. ledifolius collection sites.

Additional variation in seed dormancy might be explained by the interaction of winter precipitation with other factors such as winter temperatures and the probability of spring drought.


R^2= 0.4486
○ CEMO
● CELE
GERMINATION PERCENTAGE
100
90
80
70
60
50
40
30
20
10
0
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
WINTER PRECIPITATION (IN.)


R^2= 0.4306
GERMINATION PERCENTAGE
0
10
20
30
40
50
60
70
80
90
100
1.0
2.0
3.0
4.0
5.0
6.0
7.0
8.0
WINTER PRECIPITATION (IN.)
○ CEMO
● CELE

For example, the Uintah Basin (Utah) and northern Front Range (Colorado) have typically light winter precipitation but differ considerably in spring precipitation. The Uintah Basin has relatively dry springs, with mean March through May precipitation in Duchesne (near the Starvation and Talmage C. montanus collections) of 2.21 inches. The Front Range receives good spring moisture with mean March through May precipitation at Fort Collins (near the Fort Collins and Poudre Canyon C. montanus collections) of 5.71 inches. Dry springs favor germination under the snowpack enabling the seedling to be in a position to better utilize moisture from melting snow. Seeds adapted to such conditions will likely have a relatively rapid germination rate at near freezing temperatures. As might be expected (due to the dry winters and springs of the Uintah Basin), the Starvation and Talmage collections of C. montanus have the fastest germination rate in the cold (85 and 72% at 10 weeks of chilling). Conversely, early germination may increase the risk of seedling mortality due to spring frost. Germination delayed until the snowpack is gone would likely be advantageous regardless of the length of the effective chilling period on sites with abundant spring moisture. Seeds adapted to such sites should be relatively slow to germinate at chilling temperatures even when winter precipitation is light (short duration of snowpack). The Fort Collins and Poudre Canyon collections were relatively slow to germinate at 1°C (38 and 30% at 10 weeks of chilling) and were the only collections to have a significant increase in germination percentage after a two-week chill compared to the no-chill control (Table 2). This might suggest that the period of effective chilling is frequently quite short on the Colorado Front Range.

Although elevation of collection site is commonly used to match seed to planting site, in these experiments no correlation was found between elevation of collection site and germination percentage at 10 weeks of chilling (r^2 = 0.277 for C. montanus and 0.013 for C. ledifolius), nor germination percentage at 15°C after four weeks of chilling (r^2 = 0.149 for C. montanus and 0.083 for C. ledifolius). Clearly, elevation in these seed collections is not a useful predictor of chilling requirement.

There was considerable variability in chilling requirement among the seeds of a single collection (Tables 2 and 3). This may be related to the unpredictable and variable nature of Cercocarpus habitat.

SUMMARY

The 15 collections of Cercocarpus seeds used in this study do not require extremely long periods of chilling to germinate. Variation in chilling requirements among collections appears to be correlated with site climatic factors. Elevation does not appear to be a good predictor of chilling requirement. Regional seed sources should be used whenever possible in revegetation work. Further investigations are needed to better understand the effects of burial date, seed age, year of harvest, and known chilling requirement (in vitro) on seedling emergence and survival under a variety of field conditions.

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MINERAL-NUTRIENT RELATIONSHIPS OF THE MOUNTAIN MAHOGANIES (*CERCOCARPUS*)

Jack D. Brotherson

ABSTRACT: Data taken from the current literature and from unpublished work were used to describe the mineral-nutrient relationships of three species of mountain mahogany (Cercocarpus). General habitat and soil relationships are discussed as well as nutrient dynamics with respect to beneath and between plants, uptake patterns - soil to plant, transfer within the plant and ideas of leaf duration (evergreen vs. deciduous) in relation to nutrient conservation. The shrubs exhibited three patterns of nutrient concentration along a gradient from shrub to adjacent open area (accumulation, depletion and no change). Nutrient concentrations in the plant were significantly correlated with the available minerals in the soil. All ions became concentrated from soil to plant with phosphorus and nitrogen being the most highly magnified and micronutrients being pumped at much higher levels than macronutrients. All nutrients concentrated toward stem tip (except iron) and leaf. Four ions (N, Mg, Fe, Mn) increased in concentration from stem to leaf 1.6 times. Overall, the leaves and growing shoots had 70 times greater concentrations of nutrients than were available in the soil complex. Evergreen leaves appear to function as a nutrient conservation mechanism and allow plants (C. ledifolius and C. intricatus) to grow in highly infertile sites.

INTRODUCTION

The mountain mahoganies (Cercocarpus species H.B.K.) form a group of widely distributed native browse species of major importance in the western United States. Although their preference and palatability are low for some classes of livestock (Smith and Hubbard 1954, Sampson and Jespersen 1963), they are valuable

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as winter forage for big game animals (Medin 1960, Plummer et al. 1968). Increasing demands upon native shrubs to provide forage for both livestock and big game necessitates efficient management.

Improved management of shrubs depends upon knowledge of the ecological and nutritional aspects of the species being managed. Such information can best be gained through study of the natural ecology of shrub species. Understanding of the nutritive value of range plants managed for animal consumption is of paramount importance. Because plants are materially affected by the nature of the soils in which they grow, crops grown on different soil types vary not only in yield but also in quality, palatability, nutritive value and mineral composition (Midgley and Weiser 1936, Russell 1973).

The nutritive value of any plant is judged by the degree to which it exceeds the minimal nutrient requirements of the foraging animal. Nutritionists are concerned with the mineral content of plant tissue, because primary consumers derive the major portion of their mineral needs from plants (Harner and Harper 1973). There is a close relationship between animal health and mineral concentrations in range plants (Underwood 1971). Similarly there is close correlation between the mineral concentrations found in range plants and their soils (Brotherson and Osayande 1980). Quantitatively the nutrient needs of animals vary according to species, age, size, and activity. Because the mountain mahoganies are widely recognized as useful forage plants, knowledge of their nutritional relationships is essential for productive management. However, fundamental knowledge of the nutritional quality of these browse species is extremely limited.

Improved management of browse ranges requires that basic information be obtained on the plants providing the forage. My objectives here are to evaluate aspects of the nutrient dynamics and nutritional quality of three mountain mahogany species (C. montanus, C. ledifolius, and C. intricatus) that occur in the western United States. The data base is taken from the current literature and from published and unpublished work done in my research laboratory.

GENERAL HABITAT RELATIONSHIPS

Distribution maps for C. montanus, C. ledifolius, and C. intricatus show all three species occurring in the Intermountain West with Utah being the primary zone of overlap (Martin 1950, Pyrah 1964). Within the area of mutual occurrence the three species occupy rather distinct habitats. C. intricatus occurs on canyon walls, rimrocks, cliffs, slopes and slickrock areas in desert shrub, pinyon-juniper and mountain brush communities from 1370 m to 2400 m elevation. C. ledifolius occurs on dry, rocky ridges and slopes of southern to western exposure and in more mesic habitats than those occupied by C. intricatus. On its northern ranges it grows from 600 m to 1370 m; on southern ranges it extends from 1400 m to 3000 m elevation. It is found across its range in association with pinyon-juniper, mountain brush, aspen, and spruce-fir communities. C. montanus ranges in elevation from 1200 m to 2800 m where it occurs in sagebrush, grassland, pinyon-juniper, mountain brush, mixed conifer, and aspen communities. It is most characteristic of the "tension zone" or border between woodland and ponderosa pine types where it grows on ridges and slopes with deeper and more mesic soils than the other two species (Dayton 1931, U.S. Forest Service 1937, Medin 1960, Davis 1976, Fairchild and Brotherson 1980, Brotherson et al. 1984, Welsh et al. 1987).

GENERAL SOIL RELATIONSHIPS

Soil factors associated with habitats of the three species are shown in Table 1 (Medin 1960, Dealy 1975, Duncan 1975, Davis 1976, Greenwood and Brotherson 1978, Fairchild and Brotherson 1980). Soil depth tends to decrease from sites occupied by C. montanus through those associated with C. ledifolius to those of C. intricatus. Also, soluble salts and percents clay and silt show similar patterns of decrease across the same gradient while percent sand increases. The high levels of sand along with shallow soil depths, low levels of soluble salts, and low percents silt and clay in the C. intricatus soils indicate that this species occupies rather harsh sites of low moisture and fertility. Conversely, C. montanus tends to occupy sites that are more weathered and therefore more fertile (Brotherson et al. 1984). In general, C. ledifolius occupies sites that are somewhat intermediate to the other two species. Because weathered soils in the Colorado Plateau and Great Basin regions are generally deeper and more fertile, they are more capable of supplying nutrients to the resident species (Brotherson et al. 1984). The relationship of the recognized niches of C. montanus, C. ledifolius, and C. intricatus is illustrated in Figure 1. The model is in agreement with data published by Brotherson et al. (1984) indicating that the availability of soil nutrients to plants depends

Table 1.--Average values of selected soil factors associated with habitats of three Cercocarpus species.

Factor	C. montanus	C. ledifolius	C. intricatus
Soil depth (cm)	24.5	16.0	10.5
pH	7.3	6.9	7.2
Soluble salts (ppm)	426.0	284.0	136.0
Clay (%)	33.5	16.2	4.8
Silt (%)	37.7	25.5	9.8
Sand (%)	28.7	58.3	85.4
Fines (%)	71.2	41.7	14.6

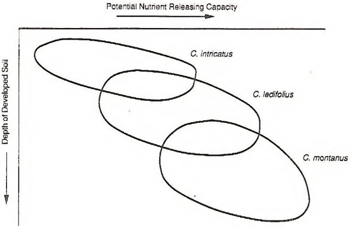


Figure 1.--Theoretical relationships of Cercocarpus species to soil depth and the potential nutrient releasing capacity of soils.

greatly on the amount and nature of nutrients in the soil solution, a result of thousands of years of physical, chemical and biological weathering. Weathering rates in turn are influenced by plant growth and by environmental factors including temperature, slope, drainage, precipitation, rates of water infiltration, general soil moisture conditions, and minerals present in the parent material (Barber 1984).

Physical weathering is important in all three habitat types. In addition, chemical and biological weathering processes appear to become more important along a gradient from the C. intricatus to the C. montanus habitat. For example, the concentrations of soluble salts in the soil are three times greater in the soils of C. montanus than in those of C. intricatus (Table 1).

MINERAL COMPOSITION - UNDERNEATH AND BETWEEN PLANTS

Observed concentrations of specific ions in the soils of C. intricatus and C. montanus (data were unavailable for C. ledifolius) are shown in Table 2. Differences between the two soils are slight with the exception of phosphorus, sodium, magnesium and calcium. Sodium and calcium concentrations are higher in the C. montanus soils while phosphorus and magnesium are higher in the C. intricatus soils. Fairchild and Brotherson (1980), in a study of the habitat relationships of six shrubs within Navajo National Monument, indicated that C. intricatus dominated slickrock areas that were consistently low in soil minerals. Similarly, C. montanus can dominate harsh sites low in soil nutrients, and also be considered a pioneer (Brotherson and Osayande 1980). Thus both

Table 2.--Average values for concentrations of selected ions in soils underneath and between shrubs of C. montanus and C. intricatus.

Mineral	C. montanus		C. intricatus	
	Under	Between	Under	Between
	ppm			
Nitrogen	552.0	406.0	540.00	327.00
Iron	7.2	4.5	4.71	3.35
Zinc	2.2	1.8	1.22	1.18
Potassium	110.0	108.0	82.50	52.80
Copper	0.6	0.6	0.38	0.30
Manganese	3.7	3.5	3.38	2.32
Phosphorus	3.8	5.3	9.16	7.14
Sodium	36.7	40.5	7.90	9.40
Magnesium	311.2	380.8	530.00	548.00
Calcium	7552.0	8866.0	1650.00	1675.00

species appear to provide avenues for the establishment of other species onto such sites, important in the long-term successional changes of those areas (Greenwood and Brotherson 1978).

Evidence indicates that shrubs influence general soil characteristics beneath their canopies (Sharma and Tongway 1973). If the influence of shrubs on various parameters of the soil surface is compared with the characteristics of the soil prior to shrub establishment, trends often become apparent. Analyses of mineral composition of soils from beneath and between C. montanus and C. intricatus plants are provided in Table 2. Samples from the open areas are an indication of the characteristics of the soil prior to shrub establishment. Ten nutrients were analyzed from soils taken from beneath and between these two shrubs. Three patterns of concentration (accumulation, depletion and no change) become apparent along a gradient from shrub canopy to adjacent open areas (Table 3). Nitrogen and iron showed enhanced concentrations beneath both species while potassium, copper, manganese and phosphorus showed enhanced concentrations only beneath C. intricatus. Conversely, zinc showed enhanced concentration only beneath C. montanus. Patterns of ion depletion beneath the shrubs include phosphorus, sodium, magnesium and calcium for C. montanus and sodium for C. intricatus. Ions showing no change include potassium, copper, and manganese for C. montanus and magnesium, zinc and calcium for C. intricatus.

An explanation of the different distribution patterns of ions between and beneath shrub canopies must include plant litter

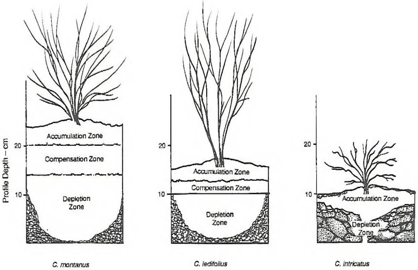
Table 3.--Enrichment ratios of ion concentrations in soils beneath and between shrubs of C. intricatus and C. montanus.

Mineral	Beneath/Between Ratio C. intricatus	 C. montanus
Nitrogen	1.7	1.3
Iron	1.4	1.6
Zinc	1.0	1.2
Potassium	1.6	1.0
Copper	1.3	1.0
Manganese	1.5	1.1
Phosphorus	1.3	0.7
Sodium	0.8	0.9
Magnesium	1.0	0.8
Calcium	1.0	0.9

fall and its decomposition, leaching of ions from plant leaves onto the soil surface with throughfall precipitation, evaporation of water from the soil surface with consequent deposition of ions on the surface and subsequent leaching into the soil profile, water movement to plant roots, transport of ions by convection and ionic diffusion, and symbiotic relations of plant roots with microorganisms (i.e., mycorrhizae and nitrogen fixation in root nodules) (Cundell 1977, Sharma and Tongway 1978, Barber 1984, Pritchett and Fisher 1987).

The distribution patterns of ions along the gradients described above parallel the three cases (accumulation, depletion and compensation) for soluble salts discussed by Sharma and Tongway (1978). Figure 2 represents a hypothetical diagram or model of how ion distribution might develop with the three Cercocarpus species and their respective soil profiles. In accumulation the ions are concentrated in the area beneath the plant canopy due to the shedding and subsequent decay of fruits and leaves from the plant. Also, direct leaching of ions from intact leaves on the plants as well as the upward transport of ions in conjunction with water evaporation from the soil surface would contribute to such accumulation. Generally, this accumulation of higher quantities of ions in the surface layers of the soil is the result of the plant taking ions from deeper in the soil profile, thus creating a depletion zone (Fig. 2). Ion depletion might also occur through their being leached out of the rooting zone entirely.

Where there is little or no change in ion concentration (compensation zone, Fig. 2), the loss of ions by plant uptake is compensated for by ions being leached downward from the enriched surface layers. Thus ion accumulation, depletion and compensation result from processes that accumulate ions in one position and deplete them from



Accumulation zone – Nutrient enrichment zone due to plant shedding fruits and leaves and their consequent decay.

Compensation zone – Zone where depletion of nutrients by plant uptake is compensated for by nutrient leachate deposition from surface layers.

Depletion zone – Nutrient depletion zone due to uptake of minerals by plant roots.

Figure 2.--Relationships among three species of Cercocarpus to soil profile depth and hypothesized zones of nutrient enrichment, compensation and depletion (after Sharma and Tongway 1973).

another. Continuous ion uptake by plants from deep in the soil, depositing them under the canopy at the soil surface, and subsequent downward leaching appears to create an endless cycle.

If the mineral nutrients are classified with respect to their degree of enrichment, compensation or depletion beneath the plant canopy in relationship to their uptake ratios (plant to soil) (Fig. 3), some interesting patterns emerge. Ions with high concentrations in the soil beneath the plant canopies are generally the same ions with high uptake in the plant (high plant/soil ratios). An exception to this pattern is phosphorus with high uptake values in C. montanus but low concentrations beneath the canopy. Also, seven of the ten mineral ions show high enrichment levels in C. intricatus (an evergreen), whereas only three of the ten are enriched in C. montanus, a deciduous species.

It is important to understand that as soil depth decreases across the gradient from C. montanus to C. intricatus (Fig. 2), corresponding changes will also occur in the accumulation, compensation and depletion zones. Generally all zones will become thinner with the compensation and depletion zones almost disappearing in the case of C. intricatus. C. intricatus is a pioneer species growing

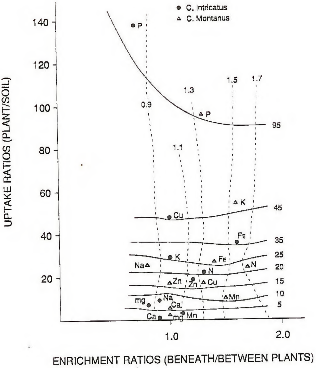


Figure 3.--Relationships between soil enrichment ratios and nutrient uptake ratios for two species of Cercocarpus.

primarily in rock crevices and outcroppings. This habitat has little or no soil development so that the depletion zone is found deep in cracks and crevices within the rock where roots can penetrate. Any soil that is found is generally in small pockets a few centimeters thick associated with the presence of plants growing out of the rock.

MINERAL UPTAKE PATTERNS - SOIL TO PLANTS

Observed concentrations of ions in the tissues of C. montanus and C. intricatus and in their respective soils (again data unavailable for C. ledifolius) are shown in Table 4. The plant-soil mineral relationships are also expressed as ratios of mineral concentrations in plant tissues to the concentrations in the soil. Uptake patterns vary widely. In all cases except calcium in C. montanus, the ions are concentrated in both species by transport from soil to plant. Plant/soil ratios varied in C. montanus from a low of 0.62 for calcium to a high of 138 for phosphorus. Patterns of ion uptake in C. intricatus are similar to those in C. montanus.

Observed differences in ion concentrations in the two plant species can generally be attributed to three factors: (1) the differential capacities of the two species for mineral absorption, (2) inherent differences in the mineral supply of the soils in which the plants grow (Russell 1973) and (3) mycorrhizal relationships and nitrogen fixation capabilities of the two species (Youngberg and Hu 1972, Lepper and Fleschner 1977, Vlamis et al. 1964). It has previously been reported that mineral concentrations in plant tissues are directly correlated with available minerals in the soils, that is, a scarcity of mineral in the soil is reflected in a corresponding scarcity in plant tissue (Beeson 1941, Russell 1973). Also, nitrogen is known to be higher in the tissue of nodulated plants (Lepper and Fleschner 1977) and mycorrhizal infections generally increase nutrient uptake in plants, especially phosphorus (Barber 1984). All such relationships are reflected in data used here, drawn from a study done in northeastern Arizona (Fairchild and Brotherson 1980) and one done in northeastern Utah (Brotherson and Osayande

Table 4.--Concentrations of mineral ions in soils and plants (current year's growth), and plant/soil mineral ratios for C. montanus and C. intricatus.

	C. montanus			C. intricatus		
Mineral	Soil	Plant	PS Ratio	Soil	Plant	PS Ratio
	------ppm------			------ppm------		
Nitrogen	406.0	9048.0	22.3	327.0	7990.0	24.4
Phosphorus	5.3	731.8	138.0	7.2	698.0	96.9
Calcium	8866.0	5486.0	0.6	1675.0	8265.0	4.9
Magnesium	381.0	2632.0	6.9	549.0	962.0	1.7
Potassium	108.0	3086.0	28.6	52.8	2830.0	53.6
Sodium	41.0	387.0	9.4	9.4	238.0	25.3
Iron	4.5	166.0	36.9	3.4	93.2	27.4
Manganese	3.5	12.0	3.4	2.3	22.2	9.7
Zinc	1.8	34.0	18.9	1.2	20.5	17.1
Copper	0.6	29.0	48.3	0.4	6.7	16.8

1980). These studies involved mineral ion concentrations in the tissue of two plant species (C. montanus and C. intricatus) and their respective soils. When the ion concentrations for ten different nutrients found in plant tissue are plotted against the corresponding concentration values from the soils, the resulting relationship ($Y = 3.55 + 0.75X$) is generally linear and significant ($p \leq 0.01$; $r^2 = 0.79$)(Fig. 4). However, plants tend to become satiated with highly concentrated soil ions and the linear relationship so apparent at lower levels of concentration becomes asymptotic. This relationship can be seen simply by removing the calcium points from the data base and redoing the regression. In so doing the r^2 improves slightly to 0.80 and the X-coefficient changes from 0.75 to 0.87. If the magnesium points are also removed from the data base, the r^2 becomes 0.85 and the X-coefficient 1.0. With an X-coefficient equalling one the proportion in the relationship being regressed with respect to the Y and X axes equals an approximate magnitude of about 23.5 to 1. Further, if the concentrations of each of the ions in the soil are regressed against their respective plant/soil concentration ratios, the relationship is negative, linear and significant ($p \leq 0.05$). Therefore, when the concentrations of essential ions in the soil are low, the plants pump many times those amounts into their tissues, but when the soil supplies are high ion concentrations in the tissues becomes less than or about equal to the soil amounts.

Except for calcium in C. montanus and magnesium in C. intricatus, the ions become concentrated in moving from soil to plant (Table 4). Phosphorus was the most highly pumped ion and was magnified in the plants an

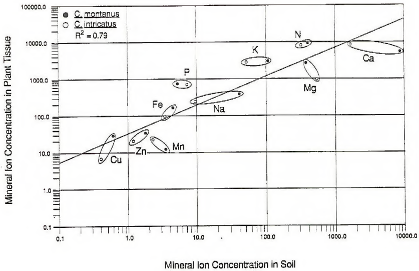


Figure 4.--Relationships between mineral ion concentrations in the soil to mineral ion concentrations in plant tissue of two species of Cercocarpus.

average of 117 times, nearly three times that of potassium and five times that of nitrogen. Such high levels of magnification, under habitat conditions of low fertility, indicates the possible presence of ectomycorrhizal infections (Pritchett and Fisher 1987). Nitrogen concentrations in the tissues of the two species (from a mean of 365 ppm in the soil to over 8500 ppm in the plant tissue) are highest of any of the nutrients studied, indicating that nitrogen fixation is taking place. The ability of the genus to fix nitrogen is well documented (Vlamis et al. 1964, Youngberg and Hu 1972, Lepper and Fleschner 1977). Because all three Cercocarpus species grow on harsh sites, where soils are generally considered to be low in fertility, the above characters may help explain the ability of these species to do well under pioneer conditions.

Figure 4 shows that the concentrations of each of the ten ions plot in highly similar patterns for both species. This is of interest because data for the two studies were taken from different habitats and soil types many miles apart and yet show the two species utilizing the individual ions in similar ways.

When the overall plant/soil concentration ratios are considered, other patterns appear (Table 5). For example, if the macronutrients (Ca, Mg, Na, K) and micronutrients (Fe, Mn, Zn, Cu) are taken as groups, the micronutrients are pumped at a rate 1.4 times that of the macronutrients. However, if potassium (a highly pumped macronutrient) and manganese (a lightly pumped micronutrient) are removed from the groups, the relationship dramatically changes with the micronutrients being pumped at

Table 5.--Mineral uptake patterns in *Cercocarpus* spp. expressed as average plant to soil ratios.

Mineral	PS Ratio
Phosphorus	117.5
Potassium	41.1
Nitrogen	23.4
Manganese	6.6
Macronutrients	16.4
Micronutrients	22.3
Macronutrients minus potassium	5.5
Micronutrients minus manganese	27.6

five times the level of the macronutrients.

NUTRIENT TRANSFER WITHIN THE PLANT

It is evident that the mineral composition of shrubs has high yearly and seasonal variation among species and individuals in natural ecosystems (Charley 1977, Fairchild and Brotherson 1980). The large differences between shrubs in arid rangelands may in part be due to the fact that uptake is highly dependent upon the amount, kind and distribution of rainfall. The variation of mineral composition in plants is partly responsible for the heterogeneous patterning of minerals in rangeland ecosystems, because soil mineral composition beneath shrubs is heavily affected by retention of litter fall, shrub age, and specific chemical composition of inorganic residues (Charley 1977). Variations in the distribution of nutrients within the plant body itself could also affect such patterns. Further, because the twig tissue of all three species of *Cercocarpus* serves as valuable forage for wildlife it is important to know the nutrient content and quality of the tissue being consumed. Table 6 contains data on the concentration of ions within three different segments of the twigs (base, middle and tip) of *C. montanus*. The data represent current year's growth only and the values are an average of 10 twigs per shrub from 10 shrubs per site across 10 sites. The patterns of distribution indicate ion concentration gradients increasing from twig base to twig tip for all ions except iron, which has an opposite concentration gradient. Iron is generally highly insoluble

Table 6.--Mineral concentrations in stems of *C. montanus*. Stem sections include base (C), middle (B) and tip (A). Values are averages and are aligned so as to flow toward the stem tip.

	Stem Sections		
Mineral	C	B	A
	------percent------		
Nitrogen	.66	.73	1.17
Phosphorus	.04	.05	.10
Calcium	.80	.93	1.40
Magnesium	.06	.07	.11
Potassium	.19	.22	.34
	--------ppm--------		
Sodium	25.9	33.6	48.7
Iron	55.2	52.1	45.6
Manganese	11.4	14.5	22.1
Zinc	26.1	29.5	39.5
Copper	6.1	6.5	9.1

under conditions of drought or where soils are calcareous (Camp et al. 1949, Rediske and Biddulph 1953). Following uptake into the plant, iron may precipitate and become somewhat immobile. That condition is heightened where high quantities of calcium ions are found in the soil solution or in the plant body (Burstrom 1968), thus iron moved rather slowly through plant tissue. This phenomenon is well illustrated when rapid growth in spring of some plant species places their new leaves in an iron deficient state indicated by chlorosis. However, as the growing season moves along the chlorosis will often disappear as the younger tissues receive additional ions of iron from internal flow within the vascular system of the plant (Mengel and Kirkby 1979).

The ratio of nutrients accumulated in parts of the plant body varies with the species as well as with the age of the individual. Ion concentrations in C. montanus (stem and leaves) along with leaf/stem ratios in current-year growth (data were taken during mid July) are shown in Table 7. The leaf to stem ratios of four ions (N, Mg, Fe, Mn) indicate an average increase from stem to leaf of 1.6 times. Five other ions (P, Ca, K, Zn, Cu) exhibit little or no pumping. These patterns are of interest because the nutrients in the first group tend to be associated with the overall processes of photosynthesis.

Nutrient accumulation within the plant body usually follows biomass expansion, increasing linearly or exponentially during periods of rapid early growth, and at a diminishing rate as the plant reaches maturity (Pritchett and Fisher 1987). The relationships between relative growth rates of plant shoots and ion influxes are complex, and the parameters directly controlling influx are yet to be identified (Barber 1984). In general, the growing shoot acts as a sink for the uptake of absorbed ions with most of the nutrients being contained in the foliage during the early growth stages (Barber 1984). Studies of nutrient flux in plant systems most often concentrate on single ion cycles and their related biology. Few references deal with the total nutrient load, corresponding influx patterns and the internal cycling dynamics within the plant system (Barber 1984). Figure 5 represents an attempt to visualize in a simple

Table 7.--Mineral concentrations in stem and leaf tissue of C. montanus. Values represent averages across populations from several sites.

Mineral	Stem	Leaf	L/S Ratio
	-------percent-------		
Nitrogen	1.00	1.40	1.4
Phosphorus	.06	.07	1.2
Calcium	1.30	1.40	1.1
Magnesium	.17	.30	1.8
Potassium	.30	.34	1.1
	--------ppm---------		
Sodium	---	---	---
Iron	488.0	764.0	1.6
Manganese	25.7	43.6	1.7
Zinc	22.9	22.7	1.0
Copper	9.0	7.8	0.9

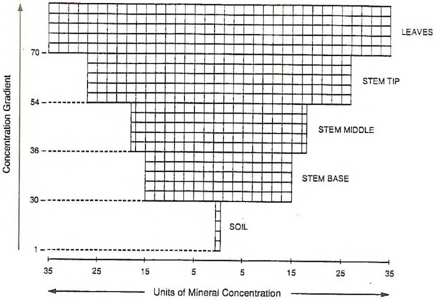


Figure 5.--Diagram of mineral nutrient flow (ten nutrients) from soil to plant twigs (stem base, stem middle, stem tip) to plant leaves. Values are ratios and are based on actual units of nutrient concentration within each classification category. Concentrations in the soil were set to be equal to one.

model the biological magnification processes of the nutrient uptake load (ten nutrients) in _C. montanus_. If all available nutrients in the soil are equal to a single unit of concentration, a mean of the plant to soil concentration ratios for all ions (Table 7) provides a clear portrayal of the overall pumping power of the plant in concentrating ions into plant tissue. Further, the flow of ions from the stem base to the leaf can be computed by adding mean ratios of ion concentration between each unit cumulatively. This gives an indication of the total ion flux into and through _C. montanus_. A concentration gradient does exist for this species; on average the leaves will have 70 times greater concentrations of ions than are available in the soil complex.

Nutrient uptake by living plant tissue can be partitioned into two categories based on the fate of the net primary production of the vegetation. One part is returned to the soil, through the death of herbaceous vegetation, leaves and twigs. In addition, appreciable amounts of ions are also leached from leaves and branches by precipitation. A second part is retained in the plant body in tissues of a perennial nature. The most consistently observed characteristic of species inhabiting infertile sites are traits that tend to reduce annual nutrient requirements, principally increased leaf longevity and a low relative growth rate. Increased leaf longevity (evergreeness) or lowered rates of leaf production is often a response to nutrient stress (Chapin 1980, Schlesinger et al. 1989). Species occupying sites of severe nutrient stress are generally dominated by evergreens while the floras of more fertile sites are dominated by deciduous types (Kimmins 1987). These patterns agree in general with the individual distribution patterns of the three species of Cercocarpus studied here.

Evergreen or deciduous traits are life history strategies involving different mechanisms for nutrient conservation (Chapin 1980). Our data (Fig. 5; Tables 6 and 7) are for the deciduous species C. montanus. Applicability of the data to the other two species of Cercocarpus, which are evergreen in nature, is problematic. It is important to remember that although the species are different with respect to leaf longevity, Figure 4 indicates that C. montanus (deciduous) and C. intricatus (evergreen) have highly similar nutrient uptake patterns.

Mooney and Gulmon's (1982) paper considering ideas relative to leaf duration has relevance to this problem. Their work suggests that C. montanus should have higher leaf photosynthetic rates, faster growth, higher leaf protein levels, and be more palatable to herbivores than C. ledifolius and C. intricatus. However, the evergreen C. ledifolius is among the most palatable of shrubs to browsing mule deer (Smith 1950, Blauer et al. 1975). Leaf duration should also help explain why C. montanus occupies habitats of higher effective moisture and greater fertility than its evergreen counterparts. The edaphic preferences of the three Cercocarpus species generally do fit expectations for deciduous and evergreen taxa, with the evergreen species occurring where nutrients are more limiting.

Plants growing in extreme environments and under conditions of low nutrient availability have evolved mechanisms for nutrient conservation, such as long foliage retention, leaching-resistant cuticles, chemical defenses against losses to herbivores, infrequent reproduction and efficient internal recycling (Chapin 1980, Kimmins 1987). In temperate regions, the annual circulation of nutrients in evergreen species is much lower than in deciduous species, largely as a result of lower leaf turnover (Cole and Rapp 1981), and lower leaching losses (Parker 1983). Nutrient reabsorption from loblolly pine needles appears to be more efficient than reabsorption from the leaves of associated deciduous species, especially when the amounts are expressed as a percentage of annual requirements. The efficiency of nutrient recovery and redistribution at the time of leaf abscission can vary according to the availability of nutrients in the soil. It has been shown that the rate of nutrient withdrawal from aging radiata pine needles was much greater on nutrient-poor soils than on more fertile soils (Florence and Chuong 1974). Trees are able to satisfy an appreciable proportion of their annual nutrient requirements by this mechanism (Kimmins 1987), resulting in greater nutrient-use efficiency in evergreen forest species. This character may offer an explanation of the frequent occurrence of evergreen Cercocarpus species on nutrient-poor sites where nutrient turnover in the soil is slow (Waring and Schlesinger 1985).

Evergreen species can retain higher levels of nutrients, particularly phosphorus, than deciduous species (Gray 1983). Evergreens almost invariably have lower nutrient levels in both live and dead leaves than deciduous species, and are more efficient at withdrawing nitrogen, phosphorus and potassium before abscission. Such internal cycling should permit greater efficiency of carbon fixation per unit of mineral resource (Small 1972). Nutrients not returned to the soil would be retained in the vegetation, corresponding to the nutrient content of living biomass added to an individual plant during the past year. It is possible that in evergreen species, such as _C. intricatus_ or _C. ledifolius_, a steady state condition may occur in which uptake would be balanced by processes that return nutrients to the soil (Collier et al. 1973). Conversely, in a species such as _C. montanus_ that occupies more fertile habitats, annual loss of leaves generally should not pose a problem nutritionally because conditions are such that nutrients would seldom be limiting.

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RESPONSE OF CURLLEAF MOUNTAIN MAHOGANY TO PRUNING IN NORTHERN UTAH 13 YEARS FOLLOWING TREATMENTS

Dennis D. Austin

ABSTRACT: Increases in forage production of curlleaf mountain mahogany (Cercocarpus ledifolius) within browsing reach of big game were sustained 13 years following pruning treatments only on summer range. Pruning treatments on winter range and girdling treatments on both summer and winter range failed to sustain increased production. On both summer and winter ranges tree mortality increased with intensity of pruning.

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INTRODUCTION

Because curlleaf mountain mahogany (Cercocarpus ledifolius) is high in nutritional value (Smith 1952, Bissell and Strong 1955, Austin and Urness 1980) especially for wintering big game (Smith 1950, Mitchell 1951, Smith and Hubbard 1954, Smith 1957), increasing its productivity could be highly beneficial. Successful efforts through seed or seedling plantings are difficult (Holmgren 1954, Plummer et al. 1957, Brown and Martinson 1959, Young et al. 1978), and bulldozing kills most trees (Dealy 1971). But pruning and girdling were shown to increase forage production for the first few years following treatment (Thompson 1970, Austin and Urness 1980). This paper reports changes in forage production and tree mortality 13 years after treatment of the original study trees as reported by Austin and Urness (1980).

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STUDY AREA

During winter 1975-76, four study sites were selected in northern Utah; two were on a lower deer winter range (1,650 and 1,820 m), one on upper winter range (2,000 m), and one on summer range (2,440 m). Each site was located on a west to northwest aspect with dry, steep slopes (40-60%). Mean precipitation ranges from about 55 cm at the lower sites to 80 cm at the upper site and occurs mostly as snow in winter. Soils were derived from limestone parent material, having rocky silt-loam textures near the surface and increasing in clay content with depth. The summer range site with a deeper profile belonged to the Typic Haploxeroll soil subgroup, while winter range sites were Lithic Haploxerolls.

METHODS

At each site 25 groups, each having 6-8 individual trees, were randomly selected and tagged. Ocular estimates of total production and forage available to big game were obtained and replicated twice. A third estimate was obtained if either set was not within 20% or 10 gm. The estimated means were then used. Plants were either pruned by hand saw at 2 m height and at intensities ranging from 0-100% foliage removal, or girdled at 2 m height. Half of all study trees had pruning paint applied to wound surfaces. Following treatment, weight estimates of the pruned trees were again obtained to determine foliage removed. Subsequent available production, below 2 m height, was estimated on all plants following the growing seasons in 1976 and 1977. Because all trees in the original study were marked with numbered aluminum tags, and all tags remained attached, the same trees were again observed in June 1988. All weights were converted to an oven-dry basis by use of dried samples.

RESULTS

Girdling

The long-term effects of girdling were negative at both the summer and winter range sites (Table 1). In the first two years following treatment forage production showed a moderate increase, but after 13 years production was reduced to less than that of control trees. Mortality of girdled trees was high: 41% on summer range and 76% on winter range. Most of the surviving trees retained one or more live branches above treatment height. Consequently girdling was determined to be ineffective for increasing forage production over the long term.

Pruning

Summer Range.--Increases in forage production on summer range were sustained 13 years after treatment (Table 1), but were not as large as in the first two years. Control trees also showed increased production. Mortality of pruned trees increased when pruning intensity exceeded about 70%. However the increase in mortality was minor when compared with the increase in forage production. Therefore, pruning of curlleaf mountain mahogany on summer range appears to be an effective method for increasing forage production over the long term.

Table 1. Mean available pretreatment production, percent change in production, and tree mortality of curlleaf mountain mahogany under various intensities of pruning and girdling.[a]

			Treatment								
					Pruning Intensity (%)						
Location	Year	Analysis	Control	Girdling	0-49	50-69	70-79	80-89	90-98	99	100
Winter Range (sites combined)	1975	Production (gm)	1.4 (80)[b]	2.2 (75)	0.8 (63)	1.1 (53)	0.6 (49)	0.9 (71)	2.8 (63)	3.3 (29)	0.0 (69)
	1976	% Change	+79	+192	+321	+521	+543	+289	+534	+889	0
	1977	% Change	+39	+337	+138	+477	+602	+683	+633	+684	--
	1988	% Change	+53	- 40	+238	- 66	+ 52	+ 32	- 20	-100	--
	1977	% Mortality	0	43	0	0	0	3	3	32	100
	1988	% Mortality	11	76	13	16	16	38	40	97	100
Summer Range	1975	Production (gm)	82.0 (25)[b]	60.4 (25)	83.4 (26)	94.7 (13)	69.3 (10)	86.5 (11)	28.0 (35)	5.0 (4)	0.0 0
	1976	% Change	+8	+11	+49	+125	+276	+345	+ 593	+917	0
	1977	% Change	+4	+24	+65	+249	+521	+822	+1317	+3535	0
	1988	% Change	+262	+185	+278	+393	+364	+506	+ 827	+1640	0
	1977	% Mortality	0	0	0	0	0	0	0	25	100
	1988	% Mortality	8	41	0	8	20	9	21	25	100

[a] Adapted from Austin and Urness (1980), with addition of 1988 data.

[b] Sample size.

Winter Range.--During the first two years following pruning on winter range, forage production was increased. In general, the higher the intensity of pruning the greater was the vegetative response. Unfortunately, the increase in forage production was not sustained after 13 years at pruning intensities exceeding 50% (Table 1). However, at lesser pruning intensities the increase in forage was sustained over the long term. Tree mortality increased with pruning intensity above 50%.

Overall, opportunities to increase browse production in mature curlleaf mountain mahogany stands on big game winter ranges via pruning appear to be minor. Large short-term increases lasting a few years occurred at pruning intensities over 50% foliage removal, and moderate long-term increases lasting at least 13 years were found to occur at pruning intensities under 50%. However because growth only occurred from live shoots (no adventitious sprouting) and weight increases in forage per tree were minor, the benefits to big game were small. Only in areas where trees have appreciable available forage within browsing reach would pruning treatments yield a practical benefit.

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EVALUATION OF CURLLEAF MOUNTAIN MAHOGANY

(*CERCOCARPUS LEDIFOLIUS* NUTT.)

STANDS 23 YEARS FOLLOWING MECHANICAL TREATMENT

Roger E. Banner, Kendall L. Johnson and Paul F. McCawley

ABSTRACT: We assessed curlleaf mountain mahogany (Cercocarpus ledifolius Nutt.) plant density and age distribution on a site in northern Utah where stands were subjected to various mechanical treatments in the winter of 1964-65. Three stand manipulation techniques--one-way dozing, one-way dozing and contour ripping, and two-way dozing of mature trees--were evaluated as methods to increase late fall-early spring browse availability for elk and deer.

Our evaluation of these stands 23 years after treatment showed that: 1) The density of curlleaf mountain mahogany is highly variable across the three mechanical treatments and the control, and appears to be related to a combination of site and treatment differences. 2) The mahogany plants growing on the control area are essentially all aged trees (>70 years old). 3) although a substantial amount of reproduction has taken place since the area was treated, more than half of the trees now present on the one-way dozed and the one-way dozed and contour ripped areas were present as young trees at the time of treatment or survived as sprouts. 4) Relatively few plants on the two-way dozed area at the time of treatment are now present, but there appears to have been good seedling survival. 5) The understory of shrub and herbaceous species on treated areas is species-rich and productive. 6) Less severe methods like one-way chaining may provide even more browse from mature curlleaf mountain mahogany stands.

At the time of the study, Roger E. Banner, Kendall L. Johnson and Paul F. McCawley were, respectively, Asst. Professor, Professor, and Asst. Professor, Department of Range Science, Utah State University, Logan. Johnson is now Head, Department of Range Resources, University of Idaho, Moscow. McCawley is now Program Leader, Range and Grazing Lands, USDA Extension Service, Washington, D.C.

INTRODUCTION

Land managers have considered habitat for wildlife an important land use for many years. They have worked together to enhance range and forest habitats important to big game and other species (Plummer et al. 1968). Large amounts of time, effort and money were spent trying to improve habitat for big game species. This often involved manipulating vegetation to increase the amounts of desirable forage available for big game species during critical times of the year.

Decadent stands of curlleaf mountain mahogany (Cercocarpus ledifolius Nutt.) on elk and deer winter ranges afford little available forage. More than 25% of the crown area is dead, tree foliage is generally beyond reach of browsing animals, and understory vegetation is sparse. During the 1960's managers were searching for effective ways to manipulate such stands to reduce the overstory of decadent trees while encouraging establishment of tree seedlings and sprouting of established trees. In the winter of 1964-65, biologists from the Logan Ranger District of the Cache National Forest and the Utah Department of Fish and Game (currently called the Utah Division of Wildlife Resources) initiated a study to evaluate mechanical methods of manipulating decadent curlleaf mountain mahogany stands. These studies were evaluated in 1965 and 1966 and served as the basis for a management plan for the Mahoganies-Pleasant Valley Area (U.S. Forest Service 1968).

SITE CHARACTERISTICS OF THE MAHOGANIES-PLEASANT VALLEY AREA

Physical Characteristics

The Mahoganies-Pleasant Valley Area is located approximately 4.8 km (3 mi) north of the Hardware Ranch Game Management Area in Blacksmith Fork Canyon, Cache County, Utah. The area is approximately 2200 m (7200 ft) above sea level with an overall south aspect and 5-25% slopes. Annual precipitation for the area is around 460 mm (18 in) occurring as both rain and snow. Soils are predominantly loams and clay loams that have formed over limestone.

Vegetation

The vegetation of the area is mixed. Common tree species include curlleaf mountain mahogany, Rocky Mountain maple (Acer glabrum), western and black chokecherry (Prunus virginiana var demissa and var melanocarpa), and serviceberry (Amelanchier alnifolia). Aspen (Populus tremuloides) and various conifers occur on north and east slopes. Mountain big sagebrush (Artemisia tridentata var vaseyana), black sagebrush (A. nova), bitterbrush (Purshia tridentata), gooseberry (Ribes montigenum), wax currant (Ribes cereum), rubber and little rabbitbrush (Chrysothamnus nauseosus and C. viscidiflorus var lanceolatus), and bearberry (Arctostaphylos uva-ursi) are common shrub species. Bluebunch, western and slender wheatgrasses (Elymus spicatus, E. smithii, and E. trachycaulus) and Great Basin wildrye (E. cinereus) are common grasses in the area. Abundant forb species include arrowleaf balsamroot (Balsamorhiza sagittata), lupine (Lupinus caudatus), Lewis flax (Linum perenne var lewisii), Oregon grape (Mahonia repens, and mulesears (Wyethia amplexicaulis) among others.

Wildlife

The area is frequented by various wildlife species. Common big game and upland game species include elk, deer, moose, snowshoe hare, blue grouse, ruffed grouse and sage grouse. Non-game species are bobcat, coyote, badger, Uinta ground squirrel, pocket gopher and porcupine as well as other small mammals, and various raptors and passerine birds.

THE HABITAT IMPROVEMENT STUDY

The Mahoganies-Pleasant Valley Area is managed under multiple-use guidelines by the U.S. Forest Service. It is used by some wildlife species year-round and extensively by elk and deer from November through April. Cattle also use the area during the month of June. The general area is popular for hunting and camping during the fall.

U.S. Forest Service and Utah Fish and Game biologists observed that young curlleaf mountain mahogany plants were more numerous in clearings and along edges of mature stands than under the tree canopy. This prompted them to consider removing decadent trees as a potential habitat improvement technique. The primary objective of the study initiated in 1964 was to change the age structure of the curlleaf mountain mahogany community by removing the tree canopy and thereby allowing young mahogany plants to become established. A secondary objective was to compare various canopy reduction practices in terms of effectiveness for plant establishment.

The study area included seven treatment locations ranging in size from 0.4 to 4.0 ha (one to 10 ac). Three mechanical treatments, each randomly assigned at two locations, and a single control were applied within the study area. The treatments were: 1) one-way dozing, 2) one-way dozing followed by ripping on the contour, and 3) two-way dozing of mature trees. The treatments were applied while the ground was frozen to minimize damage to soil and seedlings, in a year when the curlleaf mountain mahogany seed crop was exceptionally heavy. Dozed trees were left where they fell, and the study area was not protected from grazing by either wild or domestic animals.

Treatments were evaluated twice in 1965 (May and October) and again in 1966 (October). The biologists making these evaluations drew the following conclusions: 1) Although germination was high on all treatments (including the control) the first year, by 1966 the density of young curlleaf mountain mahogany plants (sprouts and seedlings) was about seven times greater on dozed plots than on the control. 2) Sprouts and seedlings were more vigorous and better developed on manipulated plots than on the control. 3) Initially, plots that were not ripped had higher densities of sprouts and seedlings than ripped plots, but by 1966, the best stands were found on the ripped plots. 4) Seedling and sprout densities were lower in duff areas where trees had stood than in other areas of the manipulated plots. 5) There was a spectacular increase in associated browse species on manipulated plots. 6) Seedling mortality was greatest on control plots.

The Mahoganies-Pleasant Valley Area Wildlife Habitat Improvement and Management Plan was developed and approved in 1968 based on conclusions drawn from the study evaluations. It was not implemented due to insufficient funding.

EVALUATION OF TREATMENTS - 1988

Methods

We evaluated the study plots in June 1988 in order to assess treatment effectiveness 23+ years after manipulation. The stand age structure and number of mahogany plants per hectare were estimated for all treatments. Age class distributions were gained by correlating trunk diameter near ground level with number of growth rings. Correlations were based on actual diameter/growth ring relationships estimated through destructive sampling.

We estimated plant densities for treated areas using the point-centered quarter method (Cottam and Curtis 1956, also described by Cook and Stubbendieck 1986). Statistical analysis procedures for assessing the trunk diameter/growth ring relationship and the estimated plant density confidence intervals followed procedures outlined by Hoshmand (1988).

RESULTS

Diameter/Number of Growth Rings (Age) Relationship

Trunk diameter and number of growth rings from plants on both cleared and uncleared areas exhibited a strong positive correlation ($P<0.01$) displayed graphically in Figure 1. The correlation coefficient (r) was 0.98.

Four size-age classes that represented trunk diameters and a range of growth rings associated with each class were identified:

Size Class I 0.1 - 1.0 cm
<11 growth rings
Size Class II 1.1 - 2.0 cm
11-16 growth rings
Size Class III 2.1 - 3.0 cm
16-20 growth rings
Size Class IV >3.0 cm
>20 growth rings.

Stand Density and Size/Age Structure by Land Treatment

Plant density for curlleaf mountain mahogany was highly variable across treatments and highest ($P<0.10$) on the two-way dozed treatment area (Figure 2). Size/age class structures by treatment are presented in figure 3.

Control.--The curlleaf mountain mahogany stands on the control (undisturbed) area were composed of trees older than 23 years (Figure 3). All 80 randomly selected plants measured were over 3.0 cm in diameter near ground level (Size Class IV). Mean trunk diameter was 21.7 cm, corresponding to an estimated age of 110 years. Only six of the 80 plants measured were less than 10.0 cm in

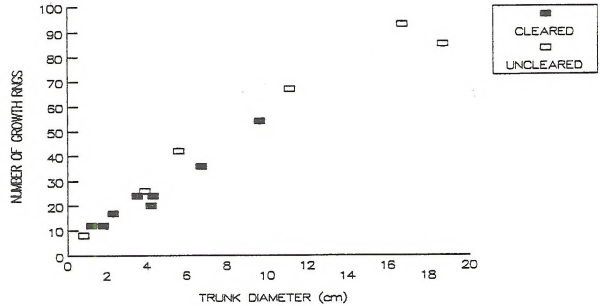

Figure 1. Relationship between trunk diameter and growth rings (correlation coefficient (r) = 0.98, P<0.01) of curlleaf mountain mahogany from both cleared and uncleared areas on the Mahoganies -- Pleasant Valley Area.

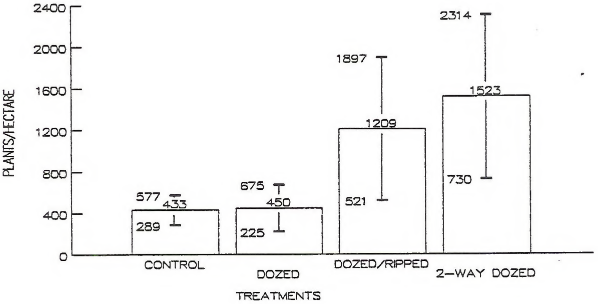

Figure 2. Densities with confidence intervals by stand of curlleaf mountain mahogany on the Mahoganies-Pleasant Valley Areas 23 years following selected clearing treatments (P=0.10).

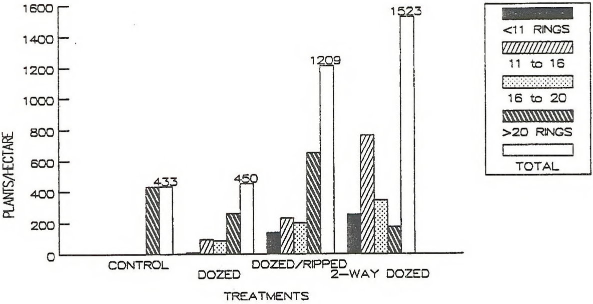

Figure 3. Size/age class structure by stand of curlleaf mountain mahogany on the Mahoganies-Pleasant Valley Area 23 years following selected clearing treatments.

diameter (±54 years old), the two smallest being 5.0 cm or about 30 years old. The largest tree measured was 49.0 cm in diameter and estimated to be 242 years old. There was little understory vegetation in these mature stands.

One-way Dozed.--On the one-way dozed treatment areas, 46 of the 80 plants measured were in Size Class IV and therefore thought to have survived the treatment (Figure 3). The largest tree measured that survived the treatment was 37.0 cm in diameter (±184 years old). Most of the remaining trees (32 of the 80 trees measured) were in Size Classes II and III; only two were estimated to be younger than 11 years old. The average trunk diameter was 5.5 cm (±33 years old). Although associated vegetation was not sampled, a variety of herbaceous and woody species associated with curlleaf mountain mahogany provided relatively high cover.

One-way Dozed/Contour Ripped.--A few more than half of the trees measured on the one-way dozed and contour ripped treatment areas (43 of 80) were 3.0 cm in diameter or larger (Size Class IV), probably old enough to have survived the treatment (Figure 3). The largest surviving tree under this treatment was 35.0 cm in diameter (±175 years old). Size Class I plants (<11 years old) made up 11.3% of the plants measured (9 of 80). Trees in Size Classes II and III (11-20 years old) made up 35% of the plants measured (28 of 80). Average trunk diameter was 5.0 cm (±30 years old). A large component of herbaceous and woody species was associated with curlleaf mountain mahogany on the treatment areas. Although contour ripping causes a substantial amount of disturbance at the time of treatment, visible evidence was not obvious after 23 years.

Two-way Dozed.--One of the two areas that were two-way dozed was a site with very shallow soils. Ecological site characteristics for this area were substantially more xeric than for the other treatment areas. Mountain mahogany plants were inconspicuous and of low density, rendering the point-centered quarter method ineffective. Therefore, we made an actual count of curlleaf mountain mahogany plants and found 78 on the 0.94 ha area. Due to these site and methodology differences, however, we decided to delete the area from the evaluation and use data from only one two-way dozed area in the analysis.

The remaining treatment area had relatively fewer surviving Size Class IV plants in the sample (9 of 40 or 22.5%) than any of the other treatments (Figure 3). Size Classes II and III (1-20 year old plants) made up 70% (28 of 40) of the plants measured. Plants estimated to be less than 11 years old made up 7.5% of the trees measured. The largest plant was 10.0 cm in diameter (±54 years old) and the average diameter for the sample was 2.5 cm (±18 years old). Again, there was a large component of herbaceous and woody species associated with curlleaf mountain mahogany on the area.

CONCLUSIONS

One-way dozing, one-way dozing with contour ripping and two-way dozing were all effective in reducing the dense canopy of mature curlleaf mountain mahogany stands. The mechanical treatments changed the size/age distribution character of treated stands toward relatively younger plants growing within reach of wintering big game animals, although only two-way dozing produced statistically greater plant densities than the control.

These treatments increased curlleaf mountain mahogany seedling establishment for a period of time and avoided destruction of young trees existing on the site at time of treatment. Treatments that incorporated one-way dozing also increased sprouting of established trees that were pushed over whereas two-way dozing killed most of the older trees. Curlleaf mountain mahogany plant establishment may be slowing on all treatments as competition from established plants of all species intensifies. Size Class I (<11 years old) plants represented 2.5%, 11.3% and 7.5% of the populations on the one-way dozed, one-way dozed and ripped, and two-way dozed areas, respectively. All treatments resulted in substantial increases in species diversity and productivity of desirable shrubs, forbs and grasses in the plant community. The net effect was a large increase in browse and forage for wintering big game.

After 23 years, there were no great differences in quality of winter habitat for big game animals among areas subjected to the mechanical treatments. However, there were substantial cost differences between treatments. Therefore, it is doubtful that one-way dozing with ripping or two-way dozing could be justified over one-way dozing alone. Because cost has precluded implementation of the habitat improvement plan, other land treatment practices should be considered for revitalizing decadent curlleaf mountain mahogany stands. Practices such as one-way chaining with debris left in place may produce an even more desirable result but at lower cost.

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THE LONG-TERM RESPONSE OF CURLLEAF MOUNTAIN MAHOGANY TO TOP PRUNING IN SOUTH CENTRAL UTAH

Robert M. Thompson

ABSTRACT: A study to evaluate pruning of mature curlleaf mountain mahogany (Cercocarpus ledifolius) trees, as a means of inducing sprouting and improving available browse for wintering big game, was established in the early 1960's in southcentral Utah. Observations of the study plots were made for 25 years; results at 5, 10, and 20 years after treatment are reported.

Longterm results indicate that limb growth and browse availability increased on spring-pruned plots over the 20-year period, variably increased and then declined on the fall-pruned plot, and suffered mortality on the winter-pruned plot. Young trees can be pruned with little mortality in spring and fall; mature trees showed minor mortality in spring, and a one in five loss in fall; old trees lost about one-quarter of their number with spring pruning and all of the fall-pruned trees. Winter pruning resulted in a loss of all trees. Young and small mature trees showed little difference in new growth over the period. Larger mature and old trees produced nearly as well for the first five years, but declined thereafter. Seedlings established mostly in open mineral soil or in shallow litter accumulations of less than four inches depth. Deeper litter must first decompose for seedlings to become established. Seedlings grew slowly and provided little available forage until late in the period.

Pruning of curlleaf mahogany trees on a large scale basis is not recommended. Treatment of smaller selected sites on critical winter range can increase available browse production if pruning is confined to the smaller and younger trees and if done in the spring or early fall. Such treatments may improve limb growth for 20 years or more, allow seedling establishment, and encourage additional available forage from associated understory vegetation.

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INTRODUCTION

Root and stump sprouting are a common response of many species of shrubs and trees to mechanical or chemical treatment. Shoot response to top pruning is also known for many species. Because curlleaf mountain mahogany (Cercocarpus ledifolius) is a key browse plant for wintering big game, and a critical need exists for additional browse, any method of increasing or improving the availability of existing browse would be helpful. Although some work had been done with curlleaf mountain mahogany, no published information was available in the early 1960's. This study was established to evaluate pruning of curlleaf mountain mahogany as a means of inducing sprouting and thereby improving available browse. Its objectives were to determine:

1. whether top pruning stimulated new limb growth and increased available browse;
2. what season or time of year was best for top pruning;
3. what size or age class of tree responded best to top pruning;
4. whether top pruning stimulated seedling establishment and improved survival;
5. how long the treatment (top pruning) remained effective.

THE STUDY AREA

Extensive stands of mature and over-mature curlleaf mountain mahogany occur on the Manti-LaSal National Forest located in south central Utah (Fig. 1). A band of trees, varying in width from a few chains to almost a mile, stretches for approximately ten miles along the east rim of Horn Mountain from Mahogany point to South Point in Emery County. Small islands of mahogany trees are scattered in various other drainages of Horn Mountain and in other parts of the Forest. All of the stands occur within key big game winter range, but in their present mature condition provide very little browse to wintering animals.

In this area of Utah, curlleaf mountain mahogany occurs at about 8,000 feet in elevation and occupies mostly the south and west-facing slopes. Annual precipitation averages 14-16 inches, and comes mostly during the winter months (October-April) as snow. Summer thunderstorms occurring during July and August account for about one-fourth to one-third of the annual precipitation.

Soils within the mahogany stands are mostly derived from the North Horn and Price River formations. They are low in fertility, shallow (0-24 inches), and of sandy to sandy loam texture. Profiles are poorly developed and structure is loose and erosive. Leaves and other organic materials accumulating near the trees break down slowly, adding relatively little to soil composition.

STUDY METHODS

In May of 1963, three one-chain (66 ft)-square plots were established in a dense stand of mahogany trees near South Point on Horn Mountain. In September and

November of 1964, two one-acre plots were established in the same general location.

On each study plot all curlleaf mountain mahogany trees were counted and age/size classified as young, mature or old. Young trees were less than four feet tall with no evidence of seed production. Mature trees were more than four but less than fifteen feet tall, stem diameter was less than five inches, and dead limbs made up less than ten percent of the crown. Old trees were more than fifteen feet tall, stem diameter was more than five inches, and dead limbs made up more than ten percent of the crown.

Three plots were pruned in mid-May, one in September, and one in late November. Trees in all plots were heavily pruned; only one or two live branches were left on each stump (Figs. 2 and 3). Several pruned branches were tagged and photographed on each study plot, as were several branches from unpruned trees adjacent to each plot. The current annual growth of each branch above the tag was measured to the nearest half inch at the close of the growing season in October.

Paired 1x100 ft strip plots were established on each of the pruned plots and on the adjacent unpruned area. The number of mahogany seedlings and other understory vegetation occurring on the strip plots was recorded.

RESULTS AND DISCUSSION

Observations and measurements were made of the pruned trees and the study plots for five growing seasons following the treatment. Results were published in Thompson (1970). Additional measurements were made for the next 20 years on the study sites; results at 5, 10 and 20 years after treatment are reported here.

Limb Growth and Browse Availability

Average limb growth on the spring-pruned plots increased from less than one-half inch before pruning to an average of 2.8 inches annual growth after pruning (Table 1; Figs. 4 and 5). Average annual growth declined slightly in succeeding years, to 2.5 and 2.3 inches at 10 and 20 years, respectively.

Trees on the fall-pruned plot showed a 2.3 inch average annual growth for the first five growing seasons of study, 3.4 inches at 10 years, and 1.4 inches over the period (Table 1). Annual growth of the fall-pruned branches is much more variable than on those pruned in the spring. Many of the pruned branches, including 6 of 20 tagged branches, died the second growing season after pruning. It was observed that the general health and condition of the fall-pruned trees was poor the first and second growing seasons, but better growth was made during the third season and seed was produced the fourth season.

Trees pruned during the winter (November-December) nearly all died before the end of the first growing season. The surviving trees had an average growth of 3.1 inches in the first year but were all dead before the end of the second growing season (Table 1).

Table 1.--Average limb growth on spring, fall, and winter top-pruned curlleaf mountain mahogany trees 5, 10 and 20 years after treatment.

	Spring		Fall		Winter	
Years	Pruned	Control	Pruned	Control	Pruned[1]	Control
	inches					
5	2.8	0.9	2.3	0.1	0	0.3
10	2.5	0.7	3.4	0.3	0	0.3
20	2.3	0.9	1.4	0.1	0	0.4

[1] No pruned trees survived beyond the second growing season.

Trees pruned during the spring bleed sap heavily. Bleeding soon stops in the smaller trees (less than 5-inch diameter), but some bleeding was still noted in the fall of the first season. Loss of sap does not seem to retard regrowth of the smaller trees, but the larger trees (6 to 8-inch diameter class) never seem to stop and usually do not live beyond the second or third growing season. While most of these large trees remain alive they do produce some regrowth. No bleeding of sap was observed from the fall or winter-pruned trees.

Pruning Season Effect

The effect of seasonal top pruning on the three age/size classes is shown in Tables 2 and 3. The young class can be top pruned without much loss when done in the spring and early fall. Mature trees show less die-off when pruned in the spring than in the fall or winter. Spring pruning resulted in 2.7 percent loss of trees after five years, whereas fall pruning resulted in 18.6 percent loss. Old trees showed 22.6 percent loss on the spring-pruned plots and 100 percent loss on the fall-pruned plots. The total loss of all trees on the spring-pruned plots amounted to 7.7 percent. The fall-pruned plots showed a loss of 34.9 percent. Winter pruning resulted in a loss of all trees.

Age/Size Class Response

The response of the three age/size classes of trees to top pruning (Table 4) was determined by measuring the new growth within each class. Young and small mature trees showed little difference in new growth produced during the first five years. Old trees produced nearly as much linear growth as the young and small mature trees for the first five years, but declined much more rapidly afterwards. They also began producing seeds much sooner than the younger, smaller trees. The new growth on the younger trees is thick and dense; on the old trees it is sparse and open. A growth progression of one study

Table 2.--Number of curlleaf mountain mahogany trees by age/size class on the spring, fall, and winter pruned plots before and five years after pruning.

Class	Spring Pruned			Fall Pruned			Winter Pruned		
	Before	After	Loss	Before	After	Loss	Before	After	Loss
	No./plot		%	No./plot		%	No./plot		%
Young	14	14	0	8	8	0	1	0	100
Mature	110	107	2.7	43	35	18.6	15	0	100
Old	44	34	22.6	7	0	100	17	0	100
Total	168	155	7.7	58	43	34.9	33	-	100

Table 3.--Age/size class composition of curlleaf mountain mahogany trees on the spring, fall, and winter-pruned plots 0, 5, 10, and 20 years after pruning.

Class	Spring Pruned		Fall Pruned		Winter Pruned	
	Yr 0	Yr 5	0	5	0	5
	percent					
Seedling	0	22.1	0	18.9	0	100
Young	8.3	7.0	13.8	11.1	3.0	0
Mature	65.5	53.4	74.1	66.0	45.5	0
Old	26.2	17.1	12.1	0	51.5	0
Class	Yr 10	Yr 20	10	20	10	20
Seedling	11.7	3.8	30.8	15.1	93.8	90.0
Young	16.1	15.1	15.4	28.3	6.2	9.1
Mature	55.6	62.5	53.8	56.5	0	0
Old	16.7	18.8	0	0	0	0

Table 4.--Average growth of curlleaf mountain mahogany trees by tree age/size class on the spring and fall pruned plots 5, 10 and 20 years after pruning.

Class	Spring Pruned Yr 5	10	20	Fall Pruned 5	10	20
	inches					
Young	3.1	2.3	2.1	2.3	2.6	2.0
Mature	2.0	1.6	1.0	2.0	2.0	1.4
Old	1.4	1.0	0.8	2.0	1.6	1.0

tree on the fall-pruned plot is shown in Figures 6 through 8.

Seedling Establishment

A large crop of curlleaf mountain mahogany seed was produced on unpruned and some pruned trees the second year after treatment. This resulted in a good crop of mahogany seedlings the following season (Table 5). Seedlings counted on the spring-pruned plots averaged 1.72 per square foot. The fall-pruned plot averaged 4.41 per square foot. No seedlings were found growing on the winter-pruned strip plot and only a few on the entire study plot.

At the end of the fifth growing season, only 0.16 seedlings per square foot (6970/acre) remained alive on the spring-pruned study plots, declining to 4356 at 10 years, and 871 trees at 20 years. On the

Table 5.--Curlleaf mountain mahogany seedlings on the spring, fall, and winter-pruned 1 x 100 ft strip plots.

Year	Spring Pruned	Fall Pruned	Winter Pruned
	no./sq ft		
2	1.72	4.41	0
5	0.16	0.38	0.05
10	0.10	0.14	0.02
20	0.02	0.06	0.01

fall-pruned plot, 0.06 seedlings/sq ft (2614/acre) persisted at 20 years, but only 0.01/sq ft (436/acre) on the winter-pruned plot. Data collected on tree density indicate that a well stocked mahogany stand in this area contains an average of 460 mature trees per acre; evidently the pruned sites are well stocked with seedlings (Fig. 9).

Many of the seedlings observed growing on both treated and untreated sites were in small bunches of 10-100 plants. Most were growing in the deep duff and litter accumulation (>5 inches) under and near the old trees. Very few seedlings were observed growing in mineral soil between the trees.

By the end of the second growing season, few of the seedlings in the deep duff or litter bunches had survived. Seedlings dug from the deep litter accumulation had many lateral roots but no central taproot, whereas those from the open and shallow litter accumulation had a strong well-developed tap root system with only a few root hairs in the top two inches below the crown. It is probable that very few of the seedlings were able to penetrate the soil below, because the soil surface was very dry. Seedling roots penetrating the litter to the dry soil surface would either die or send out lateral roots into the litter, which would later expire as the litter dried out. This condition was very pronounced among seedlings found growing in litter accumulation of more than five inches depth.

The rate at which the deep litter accumulation breaks down is very slow. No vegetation becomes established for at least three growing seasons after the litter is exposed. Annual weedy plants such as goosefoot (Chenopodium spp) and some mahogany seedlings are the first plants to establish, and continue to occupy the deep litter piles for two or three more growing seasons. Thereafter the litter becomes well decomposed and consolidated, and moisture is able to penetrate into the mineral soil for support of perennial grasses and forbs.

Understory vegetation has responded very slowly to the removal of overstory cover. Hardgrass (Elymus salinus), Indian ricegrass (Oryzopsis hymenoides), and blue grama (Bouteloua gracilis) have increased in density on all pruned plots. Mountain big sagebrush (Artemisia tridentata spp vaseyana) has increased mostly in canopy growth of the established plants. No new plants of sagebrush have been found on any study plot.

After 20 years, understory vegetation has increased enough on the spring-pruned study plot to give it a grassy aspect. Vegetation on the fall-pruned plot has not increased as much, and still has an open understory cover of grasses and some forbs.

CONCLUSIONS

1. From the results and observations made during this study, top pruning curlleaf mountain mahogany trees can result in increased limb growth and more available browse.

2. Top-pruned trees average nearly three inches of annual leader growth during the first five years after pruning. Twig growth slowed down after the third growing season. However, even after 20 years, growth on the pruned trees still exceeds that of the unpruned trees. Spring-pruned trees still averaged nearly two inches of annual growth. This is about a 200 percent increase over unpruned trees.

3. Best results from top pruning are obtained when:

   a. at least one live pruned branch is left on each pruned tree. Mahogany produces all of its new limbs from terminal growth of spurs on existing branches. No new branches sprouted from the stumps below growing limbs, indicating an absence of lower adventitious buds.

   b. pruning is done in spring (April 20-May 10) or fall (September 10-20). Late fall or winter pruning (November-January) resulted in a complete loss of all pruned trees.

   c. the smaller branches are also pruned. All heavily pruned small branches produced more regrowth than similar small branches left unpruned.

   d. the smaller mature and younger trees are pruned. Trees with stem diameters of two to four inches and less than 12 feet tall are the easiest to prune, give better regrowth, and suffer less mortality. Large overmature trees are very difficult to prune and have fewer branches suitable for pruning. They also bleed heavily and many die soon after pruning.

4. Seedlings growing in the pruned study plots are mostly established in the open mineral soil or in shallow litter accumulations of less than four inches depth. However, after five growing seasons, the deeper litter accumulation breaks down enough for seedlings to become established.

5. Seedlings four to five years old average only four to ten inches in height. At this state, they provide very little available forage and are only lightly grazed. Snow cover also protects them from grazing. After 20 years, many of the first-established seedlings are now two to three feet tall and are providing considerable available browse.

6. A well stocked mahogany stand in this area averages about 460 mature trees per acre. The spring-pruned study plot with its present number of seedlings (after 20 years) would have about 1900 stems per acre. The fall-pruned plot would have about 1750 stems per acre, and the winter-pruned plot about 700 stems per acre.

7. Large scale top pruning of curlleaf mahogany stands is not recommended. Pruning smaller selected sites (one to two acre size) that have mostly small (two to four

inch diameter stem size and not over eight feet tall) mature age class of trees can result in increased limb growth and improved browse production. Pruning small selected sites on critical big game winter range could increase available browse production while not reducing essential big game cover or changing the general aspect of the site.

8. The short-term benefits of top pruning curlleaf mahogany trees are (1) pruning can result in over 200 percent increase in available browse during the first five years after pruning, (2) establishment of new seedlings can provide future browse, and (3) opening stagnant stands can increase understory vegetation.

The long-term benefits of top pruning are (1) continuous improved growth for 20 years or more, (2) established seedlings providing additional browse, and (3) understory vegetation providing improved ground cover and additional available forage.

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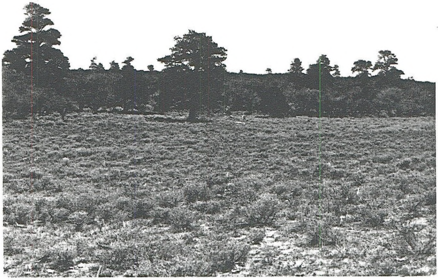

Figure 1.--General view of curlleaf mountain mahogany stands, South Horn Mountain, Manti-LaSal National Forest.

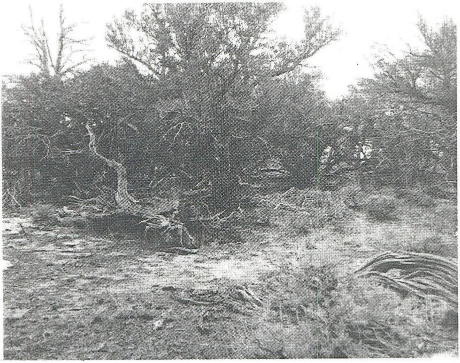

Figure 2.--Over mature curlleaf mountain mahogany trees on spring-pruned plot 3 prior to pruning. Note density of tops and numerous dead limbs.

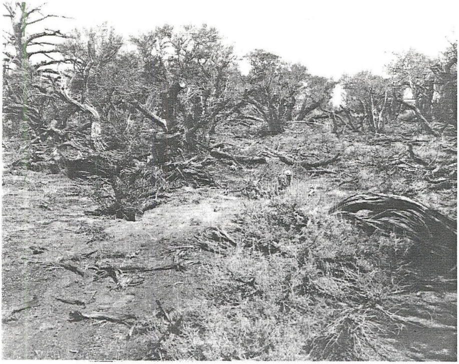

Figure 3.--Spring-pruned plot 3 immediately after pruning. Note size of limbs cut. Height to first small branches is about four feet - nearly out of reach to most browsing animals.

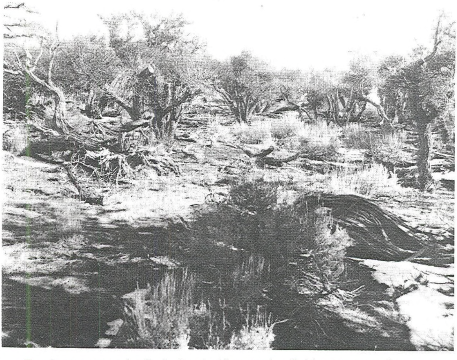

Figure 4.--Spring-pruned plot 3 at the end of three growing seasons after pruning. Pruned trees averaged 3.5 inches of annual growth. Only one pruned tree died on this plot.

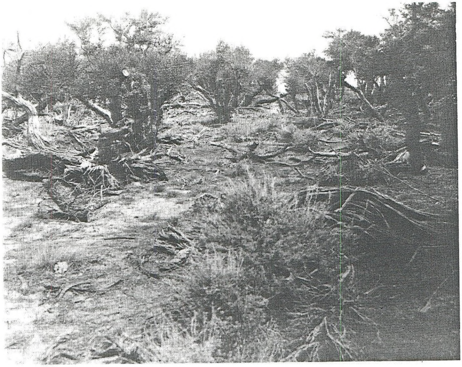

Figure 5.--Spring-pruned study plot 3 after five growing seasons following treatment. Pruned trees averaged 2.8 inches of growth annually, a 200% increase in available browse.

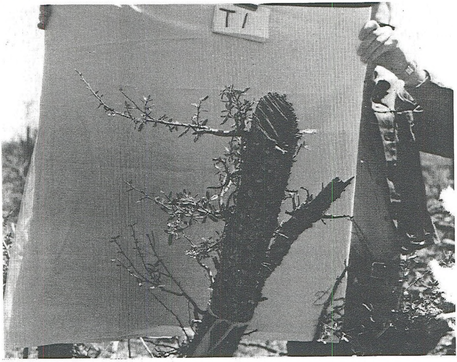

Figure 6.--Study tree T-1 on the fall-pruned plot immediately after pruning.

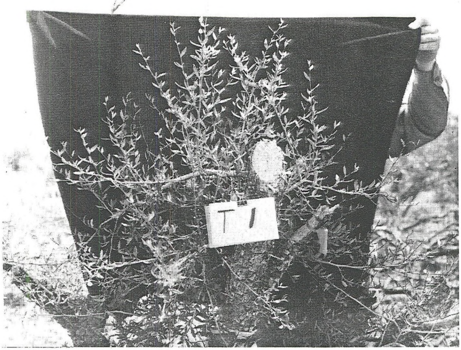

Figure 7.--Study tree T-1 on the fall-pruned plot five growing seasons after pruning. This branch was growing at an average rate of 3.3 inches per season.

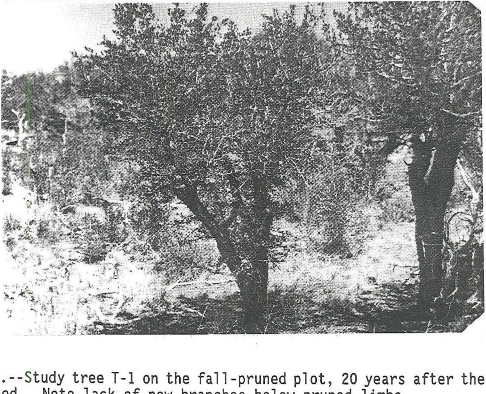

Figure 8.--Study tree T-1 on the fall-pruned plot, 20 years after the tree was pruned. Note lack of new branches below pruned limbs.

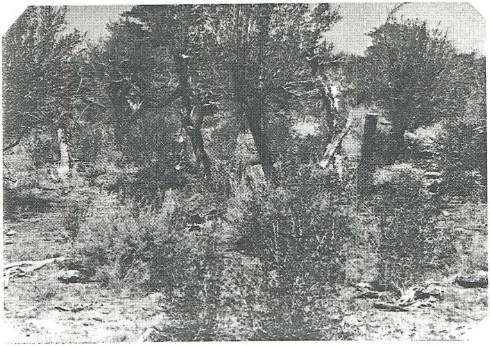

Figure 9.--Young plants that have become established since the pruning are nearly two feet tall and are growing rapidly at 6-8 inches annually 20 years after treatment. Some big game use is now being made of most of the seedlings on this site.

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Utah Shrub Ecology Workshop. Utah State Univ., Logan.

STAGNATION AND DECADENCE OF *CERCOCARPUS MONTANUS* IN A SOUTHEASTERN WYOMING BIG GAME EXCLOSURE

William J. Waugh

ABSTRACT: A study was conducted to determine whether annual shrub production within a big game exclosure, located within a mountain big sagebrush/true mountain mahogany association in southeastern Wyoming, had stagnated after 40 years of nonuse. Sampling for percent canopy cover, annual production, shrub density, age-size class, and percent dead material was done within a homogeneous stand inside and outside the exclosure.

Differences in percent canopy cover and shrub density were insignificant for both species. Current year's sagebrush production was no different inside vs. outside the exclosure, but was significantly greater outside than inside for mountain mahogany. The protected mountain mahogany produced much less biomass inside the exclosure than outside. It appears that some utilization is necessary for optimum production of mountain mahogany, and that protected areas do not necessarily define the 'climax' condition of mountain shrubs.

INTRODUCTION

Range resource managers often use various types of exclosures in studies of forage production and utilization, range condition and trend, watershed protection, and soil conservation (Hanson 1952).

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Daubenmire (1940) defined an exclosure as, "...any experimental area which is protected from the activities of a particular class of animal by a barrier such as a fence or screen." Stoddard et al. (1975) suggested that an ideal method for quantifying range condition was to compare species composition and relative abundance data collected within an exclosure, that has been in place for many years, with corresponding data collected in an unprotected area with similar site characteristics. The vegetation within long established exclosures has often been considered to be in a "climax" state, in excellent condition. The range condition on similar sites has been scored as poor to excellent depending on how similar it was to this "climax" indicator. Annual forage production is often determined as the differences between the biomass of selected species "inside versus outside" both permanent and temporary exclosures.

The results of two previous studies of browse production and utilization in the Intermountain Region contradict this general assumption that with time, protected vegetation can be measured as an indicator of optimum forage production; and that "climax," as represented in permanent exclosures, should be the goal of management. Tueller and Tower (1979) found that productivity of some major browse species decreased significantly, or stagnated, when an area was protected from large ungulate browsing. Martinson (1960) found bitterbrush to produce substantially less annual biomass when left unbrowsed for several years.

In southeastern Wyoming, true mountain mahogany (Cercocarpus montanus) is considered to be an important browse species on mule deer winter range. A big game exclosure constructed by the Civilian Conservation Corps, in the late 1930's, is located in a mountain big sagebrush (Artemisia tridentata ssp. vaseyana) true mountain mahogany association on the eastern slope of Sheep Mountain, southwest of Laramie. The purpose of this investigation was to determine whether annual shrub production within the exclosure had stagnated after 40 years of nonuse.

DESCRIPTION OF THE STUDY AREA

The study area was located 2 kilometers west of Wyoming Highway 230, 39 kilometers southwest of Laramie, Wyoming. The big game exclosure, constructed with 2.4 meter woven wire fencing, was located just west of a rail fence marking the Medicine Bow National Forest boundary on the east slope of Sheep Mountain. At an elevation of 2430 meters, the exclosure had an area of approximately 1.0 hectare, an aspect of N 80° E, and an average slope of 22 percent. The vegetation, as classified by Porter (1962), was foothill shrub. This area is considered to be important elk and mule deer winter range. The recent history of use is indicated by hedged mountain mahogany and a distinct browse line on juniper adjacent to the exclosure. Shrubs, forbs, and grasses identified at the study area are given in the Appendix. Common names follow Beetle (1970).

METHODS

A relatively homogeneous big sagebrush/mountain mahogany stand along the northern fence of the exclosure was selected for study. It was necessary to select a stand divided by the fence so both browsed and unbrowsed conditions could be sampled. Sampling plots were located within the stand using a stratified random design (Knight 1978). Baselines were located 3 meters away from the exclosure fence, both inside and outside, to eliminate the effects of fence construction and drifting snow (Fig. 1). Five transect lines were placed perpendicular to each baseline at 3 meter intervals. Sampling points were randomly located along each transect. Random numbers represented the distances between quadrats. If the number selected was even, the quadrat was placed on the right side of the transect, if odd, on the left side.

Sampling was done in October 1980, following the growing season and prior to the period of greatest deer use. Percent canopy cover and annual production were estimated within 1.5 by 1.2 meter plots using a modification of the technique described by Fisser et al. (1977) for sampling arid land shrubs. A sampling frame consisting of eighty 15 by 15 cm sections was cut from standard concrete reinforcement mesh. Percent canopy cover was recorded as units per quadrat for each shrub species (each 15 by 15 cm section of the frame represented a sampling unit). Annual production was estimated as units per quadrat and current year's growth of each shrub species was clipped in three representative units along each transect. Annual production was calculated both inside and outside the exclosure by multiplying the mean air-dry unit weight for each shrub by the total number of production units recorded. The resulting number was converted to kilograms per hectare.

Shrub density, age/size class, and percent dead material were also estimated inside and outside the exclosure. Each shrub located within a quadrat was assigned an age/size class (1 = seedling, 2 = young and small, 3 = intermediate size, 4 = mature, 5 = old and decadent). The percent dead material for each shrub within each plot was visually estimated.

RESULTS AND DISCUSSION

Percent canopy cover, current year's production, age/size class, and percent dead material for the stand both inside and outside the exclosure are provided in Table 1. Only true mountain mahogany and mountain big sagebrush results are given because the occurrence of other browse species was too infrequent for adequate comparison.

The results of student's t-tests ($\alpha = 0.1$) for significant differences between the shrubs inside and outside the exclosure revealed the following:

- Percent canopy cover differences were not significant for either mountain mahogany or sagebrush.
- Annual production, the weight of air dried clippings of current year's stem elongation, was significantly greater outside for mountain mahogany than inside. Current year's sagebrush

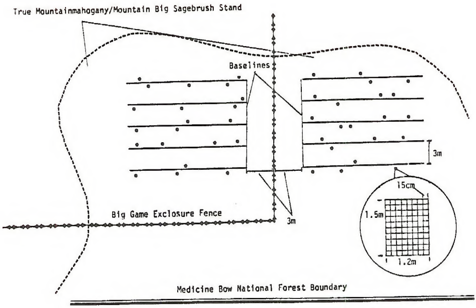
True Mountainmahogany/Mountain Big Sagebrush Stand
Baselines
3m
15cm
1.5m
1.2m
Big Game Exclosure Fence
3m
Medicine Bow National Forest Boundary

Figure 1. Stratified random method for sampling vegetation in a true mountain mahogany/mountain big sagebrush stand divided by a big game exclosure fence.

Table 1.--Density, canopy cover, production, and percent dead material for true mountain mahogany and mountain big sagebrush inside and outside a big game exclosure in southeastern Wyoming.

	True mountain mahogany		Mountain big sagebrush	
	Inside Exclosure	Outside Exclosure	Inside Exclosure	Outside Exclosure
Mean Density (Plants/m^2)	1.10	0.82	1.40	1.26
Canopy Cover (x Percent)	4.4	5.7	10.7	7.9
Production (Kg/ha)	107.8	242.3[1]	484.4	422.5
Dead Material (x Percent)	43.5	18.7[1]	22.3	18.2

[1] Significant difference between inside and outside values ($\alpha = 0.1$)

production, inside versus outside, was not significant.

- Density differences inside versus outside the exclosure were insignificant for both shrub species.
- Mountain mahogany plants inside the exclosure appeared older, larger and had a significantly greater percentage of dead stems and branches than plants outside the exclosure.

Looking along the fenceline of the exclosure, there appeared to be considerably greater total mountain mahogany biomass inside than outside. However, the results indicate that the protected stand inside the exclosure produced 52 percent less biomass in 1980 than the browsed stand outside. This difference in annual production was obvious. The current year's shoot growth on the hedged plants outside appeared much greater than on the tall, spindly plants inside. Also, the protected stand appeared decadent, there were many dead stems and very few, if any, young plants.

It appears from these results that some browsing pressure is necessary for optimum sustained yield of true mountain mahogany. Ferguson and Basile (1966) speculated that the physiological response of bitterbrush to removal of the apical meristem stimulated new shoot growth in the dormant axillary buds. The initial imbalance in shoot-to-shoot ratios after browsing creates a relative abundance of soil moisture and nutrients. The net effect is a reduction in root growth and an increase in shoot growth at the axillary buds until shoot-to-shoot ratios are reestablished. Before browsing, apical shoots tend to have long internodes while axillary shoots are short. When the apical bud is removed, the axillary buds begin producing shoots with long internodes. The net effect is a change from a single long shoot to several long shoots and an increase in current year's biomass production.

Another possible reason for the observed differences in production is increased interspecific competition within the exclosure. Grasses and forbs protected from foraging cattle and other large ungulates may be healthier and more competitive for available moisture and nutrients, thereby limiting shrub growth and reproduction.

CONCLUSIONS

This study complements similar studies of bitterbrush, willow, and mountain mahogany showing that nonuse for several years results in growth stagnation. The following inferences relative to management practices can be made:

- The steady state "climax", as represented by vegetation protected from use in exclosures for extended periods, is not necessarily the most desirable range condition for the mountain mahogany type.
- Similarly for the mountain mahogany type, estimates of potential productivity, annual production, and utilization may be confounded when permanent exclosures are used. Temporary (single season) cage exclosures may provide more accurate production and utilization information.
- Some level of use is necessary for maximum sustained yield on mountain mahogany winter range.

Future studies of true mountain mahogany growth stagnation and stand decadence resulting from nonuse should address overstory/understory relationships, optimum browsing pressure for sustained maximum regrowth, and rates of ecological succession.

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Appendix.--Plant species identified in the Sheep Mountain Exclosure include:

SHRUBS

Amelanchier anifolia	Saskatoon serviceberry
Artemisia tridentata (ssp. vaseyana)	Mountain big sagebrush
Berberis repens	Creeping barberry
Cercocarpus montanus	True mountain mahogany
Chrysothamnus nauseosus	Rubber rabbitbrush
Chrysothamnus viscidiflorus	Douglas rabbitbrush
Juniperus scopulorum	Rockymountain juniper
Leptodactylon pungens	Granite pricklygilia
Opuntia polyacantha	Plains pricklypear
Purshia tridentata	Antelope bitterbrush
Symphoricarpos occidentalis	Western snowberry
Tetradymia canescens	Grey horsebrush
Xanthocephalum sarothrae	Broom snakeweed

FORBS

Arabis holboellii	Holboell rockcress
Ceratoides lanata	Common winterfat
Cryptantha bradburiana	Minerscandle cryptantha
Descurainia pinnata	Pinnate tansymustard

GRASSES

Agropyron smithii	Western wheatgrass
Agropyron spicatum	Bluebunch wheatgrass
Koeleria cristata	Prairie junegrass
Oryzopsis hymenoides	Indian ricegrass
Stipa comata	Needleandthread

DESCRIPTION AND DISCUSSION OF FIELD TOUR SITES

Roger E. Banner

INTRODUCTION

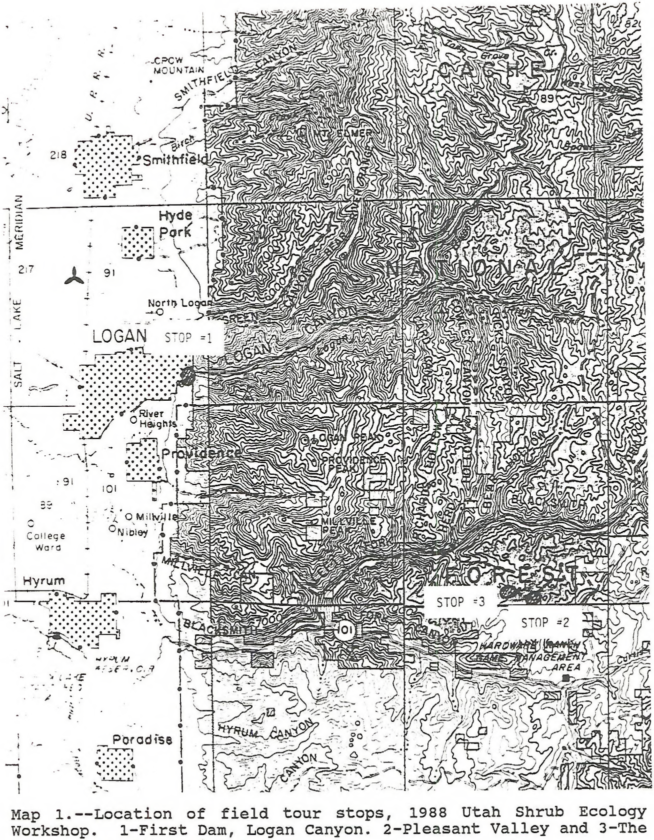
The field tour of the 1988 Utah Shrub Ecology Workshop centered on mountain mahogany populations in Cache County, Utah. It included a stop at the mouth of Logan Canyon and stops in the Pleasant Valley and Mahoganies areas northwest of Hardware Ranch (Map 1). First, tour participants observed and discussed morphological and ecological characteristics of three mountain mahogany species. Second, they visited locations where various treatments had been applied to stimulate mature curlleaf mountain mahogany stand rejuvenation.

Howard Stutz of Brigham Young University, Al Winward of the Forest Service Intermountain Region and Roger Banner of Utah State University led discussion at the various stops.

STOP 1. FIRST DAM, MOUTH OF LOGAN CANYON

Al Winward introduced the group to the general area when the tour participants gathered along US Highway 89 near First Dam, at the mouth of Logan Canyon. Three species of mountain mahogany occur at this location: Curlleaf mountain mahogany (Cercocarpus ledifolius) on both north and south slopes of the canyon; true mountain mahogany (C. montanus) on the north slope; and little leaf mountain mahogany (C. intricatus) on the south slope (Fig. 1-3).

Howard Stutz described the interbreeding of the three species in the area. He informed tour participants that curlleaf and true mountain mahoganies were interfertile, and that the resulting hybrid had evolved into little leaf mountain mahogany. He discussed the genetic



Map 1.--Location of field tour stops, 1988 Utah Shrub Ecology Workshop. 1-First Dam, Logan Canyon. 2-Pleasant Valley and 3-The Mahoganies, Blacksmith Fork Canyon.

plasticity of curlleaf mountain mahogany and pointed out the broad range of leaf types occurring on individual plants. The group located individual plants having leaves characteristic of each of the three species. Stutz commented that this was a graphic and dramatic example of the evolutionary process in progress.

Al Winward pointed out hybrids resulting from black sagebrush (Artemisia nova) and mountain big sagebrush (A. tridentata ssp.vaseyana) also found on the area. The group discussed the potential for possible breeding work on native species.

STOP 2. THE PLEASANT VALLEY AREA NORTHWEST OF HARDWARE RANCH

After regrouping at Hardware Ranch, in the Blacksmith Fork Canyon on State Highway 101, the tour participants proceeded to the Pleasant Valley area, an important seasonal range for deer, elk and moose. The group observed a number of curlleaf mountain mahogany trees that had been topped in an effort to stimulate sprouting and thereby increase the availability of browse for wintering animals. The practice was deemed unsuccessful because the treatment killed some trees while stimulating only limited sprouting on others.

Howard Stutz led a discussion of the key morphological characteristics used in the taxonomic classification of curlleaf mountain mahogany. He also outlined the distribution of this species indicating that it extends to the West Coast.

Al Winward showed tour participants mountain rubber rabbitbrush (Chrysothamnus nauseosus ssp. salicifolius) growing in the area. It is a palatable subspecies of rubber rabbitbrush commonly found in association with curlleaf mountain mahogany.

STOP 3. THE MAHOGANIES AREA NORTHWEST OF HARDWARE RANCH

The tour participants proceeded to the Mahoganies, an area where a study of mechanical treatments to rejuvenate mature curlleaf mountain mahogany stands was initiated in the 1960's. The treatments applied on the area were one-way dozing, one-way dozing with ripping, and two-way dozing. An evaluation of these treatments by Roger Banner, Kendall Johnson and Paul McCawley in 1988 is reported in this proceedings.

Roger Banner introduced the group to the area outlining the practices that were applied. The group walked over plots representative of each of the mechanical treatments (Fig. 4-6) as well as an undisturbed area (Fig. 7) to note the plant densities and note the plant densities and age class distributions for curlleaf mountain mahogany and associated species. Banner reviewed the evaluation results presented in the workshop and led a discussion of the general effectiveness of the various practices. The group observed and discussed the apparent relative success of the treatments in stand rejuvenation. The participants also noted and discussed the richness and productivity of associated species on treated areas, and suggested that less severe and less expensive practices may be even more desirable (Fig. 8).

In: Johnson, K. L. (ed.). 1990. Proceedings of the fifth
Utah Shrub Ecology Workshop. Utah State Univ., Logan.

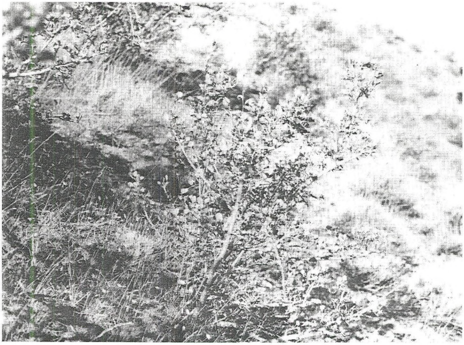


Figure 1.--True mountain mahogany (Cercocarpus montanus) growing on a north slope at the mouth of Logan Canyon.

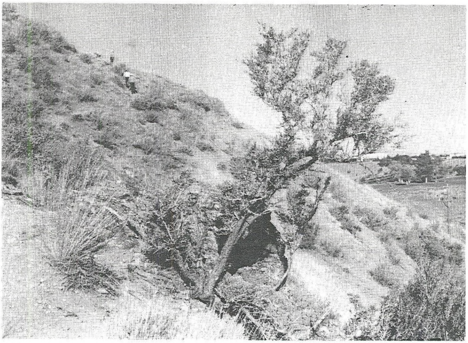


Figure 2.-- Curlleaf mountain mahogany (Cercocarpus ledifolius) growing on a north slope at the mouth of Logan Canyon.

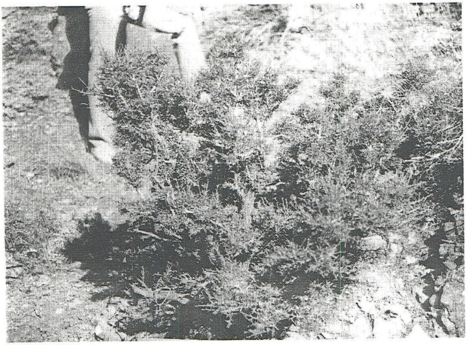


Figure 3.--Little leaf mountain mahogany (Cercocarpus intricatus) growing on a south slope at the mouth of Logan Canyon.

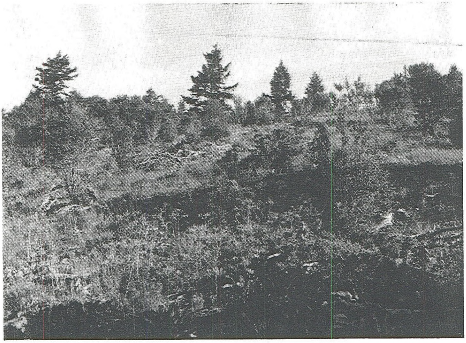


Figure 4.--One-way dozed curlleaf mountain mahogany stand 23 years following treatment.

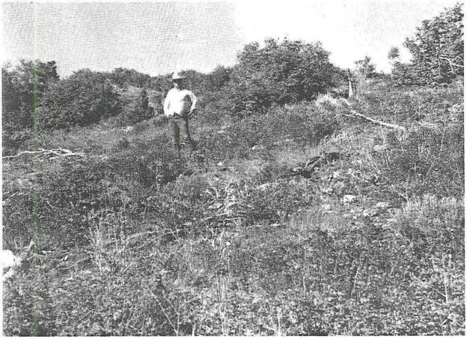


Figure 5.--One-way dozed and ripped curlleaf mountain mahogany stand 23 years following treatment.

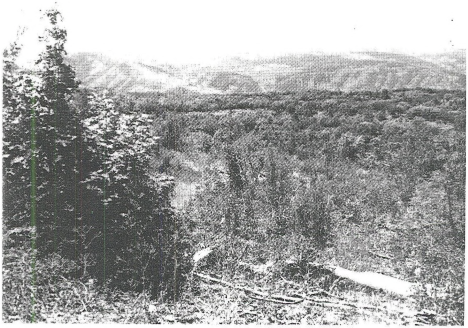


Figure 6.--Two-way dozed curlleaf mountain mahogany stand 23 years following treatment.

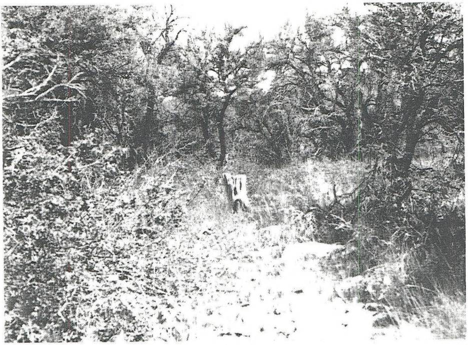


Figure 7.--Untreated stand of mature curlleaf mountain mahogany.

Figure 8.--Tour participants having lunch at the edge of a mature stand of curlleaf mountain mahogany.

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1981 Sanpete County
Big Sagebrush
Richard Stevens, DWR
Field Chairman

1982 Millard County
Pinyon-juniper
Harvey D. Gates BLM
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Field Chairmen

1983 Utah County
Gambel Oak
Arthur R. Tiedemann INT
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1986 Iron County
Rabbitbrush
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